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Do soil organisms affect aboveground litter decomposition in the semiarid Patagonian steppe, Argentina?

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Abstract Surface litter decomposition in arid and semiarid ecosystems is often faster than predicted by climatic parameters such as annual precipitation or evapotranspiration, or based on standard indices of litter quality such as lignin or nitrogen concentrations. Abiotic photodegradation has been demonstrated to be an important factor controlling aboveground litter decomposition in aridland ecosystems, but soil fauna, particularly macrofauna such as termites and ants, have also been identified as key players affecting litter mass loss in warm deserts. Our objective was to quantify the importance of soil organisms on surface litter decomposition in the Patagonian steppe in the absence of photodegradative effects, to establish the relative importance of soil organisms on rates of mass loss and nitrogen release. We estimated the relative contribution of soil fauna and microbes to litter decomposition of a dominant grass using litterboxes with variable mesh sizes that excluded groups of soil fauna based on size class (10, 2, and 0.01 mm), which were placed beneath shrub canopies. We also employed chemical repellents (naphthalene and fungicide). The exclusion of macro- and mesofauna had no effect on litter mass loss over 3 years ($P = 0.36$), as litter decomposition was similar in all soil fauna exclusions and naphthalene-treated litter. In contrast, reduction of fungal activity significantly inhibited litter decomposition ($P < 0.001$). Although soil fauna have been mentioned as a key control of litter decomposition in warm deserts, biogeographic legacies and temperature limitation may constrain the importance of these organisms in temperate aridlands, particularly in the southern hemisphere.

Keywords Aridlands · Macro- and mesofauna · Fungi · Carbon turnover · Termites

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Introduction

Plant litter decomposition is a key process in terrestrial ecosystems, determining carbon turnover, as well as the rate and timing of nutrient release. While climate and litter chemistry have been shown to be some of the most important factors controlling litter decomposition in terrestrial ecosystem at the regional scale (Meentemeyer 1978; Vitousek et al. 1994; Coûteaux et al. 1995; Austin and Vitousek 2000; Gholz et al. 2000; Cornwell et al. 2008; Bontti et al. 2009), soil organisms (soil fauna and microbes) represent a key biotic component affecting soil organic matter formation and nutrient release locally (Swift et al. 1979; Coûteaux et al. 1995; Aerts 1997). Soil fauna have body sizes large enough to disrupt physical structure of soil and litter and can affect organic matter decomposition directly through fractionation and consumption of litter (Coleman and Crossley 1996). In addition, they can affect decomposition indirectly through changes in microclimate conditions such as soil moisture and litter surface area, regulating microbial activities during litter decomposition (Bradford et al. 2002).

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Surface leaf litter decomposition in many arid and semiarid ecosystems has shown little correlation with climatic parameters such as precipitation and evapotranspiration (Whitford et al. 1981; Steinberger et al. 1990; Hamadi et al. 2000; Vanderbilt et al. 2008; Austin 2011) or litter quality (Schaefer et al. 1985; Steinberger and Whitford 1988; Austin 2011). Several alternative controls have been proposed to explain the discrepancies of litter mass loss in arid and semiarid ecosystems with global climatic and litter quality models. First, beyond the actual amount of precipitation inputs, the pulsed nature of precipitation events in aridlands has been identified as an important factor affecting organic matter decomposition, through the dry/wet cycles that affect organic carbon turnover (Austin et al. 2004; Collins et al. 2008), and through the instantaneous response of microbes to soil moisture changes (Schwinning and Sala 2004). Additionally, some recent studies have quantified that photodegradation, the photochemical mineralization of organic matter, is a driver of carbon loss in aridlands (Austin and Vivanco 2006; Brandt et al. 2009; Rutledge et al. 2010). As photodegradation functions largely independently of precipitation inputs, it could explain the higher rates of litter mass loss in aridland ecosystems, which usually receive larger solar radiation inputs than mesic and humid ecosystems (Austin and Vivanco 2006; Throop and Archer 2007).

In addition, soil fauna (macro- and mesofauna) have been postulated as an important control of litter decomposition in aridlands, with effects on decomposition that are disproportionate with respect to their biomass. In particular, termites and ants in some warm deserts have been identified as key players responsible for high rates of litter mass loss and nutrient release in these ecosystems (Santos and Whitford 1981; Schuurman 2005; Wagner and Jones 2006; Ginzburg et al. 2008). Several studies have demonstrated a significant reduction in leaf litter decomposition when soil fauna have been intentionally manipulated or excluded in tropical and subtropical forests (Yamashita and Takaeda 1998; Green et al. 1999; Heneghan et al. 1999; González and Seastedt 2001; Höfer et al. 2001; Yang and Chen 2009), and grasslands (Vossbrinck et al. 1979; Bradford et al. 2002; Smith and Bradford 2003; Wall et al. 2008). However, the effect of soil fauna on litter decomposition at a global scale is not strongly apparent, as a global study of their impacts showed modest and biome-specific effects of the exclusion of mesofauna (Wall et al. 2008).

Several studies have also suggested a key role for fungi in litter decomposition in aridlands. The preponderance of stochastic precipitation pulse events (Collins et al. 2008), and low concentrations of soil organic matter distributed in patches (Schlesinger et al. 1996; Austin et al. 2004; Gonzalez-Polo and Austin 2009), provide a suite of conditions with advantages for fungi, which exhibit high desiccation tolerance (Wilson and Griffin 1975) and an ability to thrive in relatively dry conditions (Went and Stark 1968). For instance, in a recent study in a semiarid Mediterranean ecosystem, fungi resisted simulated drought more successfully than bacteria, with direct implications for soil organic matter turnover (Yuste et al. 2010). In addition, a selective reduction in the soil microbial community has demonstrated substantial reductions in litter decomposition (Santos and Whitford 1981; Parker et al. 1984). This evidence suggests that fungal abundance and activity may be important affecting litter decomposition in warm desert ecosystems.

The Patagonian steppe is a semiarid ecosystem with vegetation of a mixture of shrubs and grasses interspaced in a bare soil matrix (Golluscio et al. 1998). Soil organic matter is also heterogeneously distributed in the landscape (Austin et al. 2006; Gonzalez-Polo and Austin 2009). Aboveground litter decomposition in open areas in this ecosystem has been shown to be controlled principally by abiotic photodegradation (Austin and Vivanco 2006), but the relative contribution of soil fauna and fungi on the decomposition process in the Patagonian steppe has not been explicitly evaluated. The patchy distribution of vegetation results in two distinct microsites where bare soil patches are exposed to high levels of solar radiation and vegetated patches have high concentrations of soil resources, microbial biomass and soil enzymatic activity (López et al. 2003; Gonzalez-Polo and Austin 2009). These vegetation microsites also differentiate the feeding patterns by granivorous ants and habitat use by beetles (Folgarait and Sala 2002; Mazía et al. 2006), and in particular, darkling and ground beetle (Tenebrionidae, Carabidae) activity is greater beneath shrubs than in bare soil areas (Mazía et al. 2006).

The objective of this study was to quantify the relative importance of soil organisms on aboveground litter decomposition in vegetated patches of the semiarid Patagonian steppe. We predicted that: (1) soil fauna (macro- and mesofauna) have an important impact on litter decomposition, and their exclusion would significantly decrease rates of mass loss; and (2) fungi play a key role in biotic litter decomposition, and the reduction of fungi populations from soil and litter would significantly decrease the rate of mass loss. Our experimental approach was to manipulate the access of soil organisms to decomposing litter as a function of body size (Anderson 1988), using different mesh sizes and chemical repellents to restrict the access of specific functional groups of soil fauna to the litter. In addition, we examined the consequences of reducing fungi from soil and litter on the dynamics of litter decomposition and nutrient release.

Materials and methods

Study site

The experiment was conducted at the Río Mayo experimental station of the National Institute for Agricultural Technology (INTA), a semiarid temperate shrub-steppe, in the Patagonian region of Argentina (45°41′S, 70°16′W). Average annual precipitation is 170 mm, occurring primarily during autumn and winter (March to August). Mean monthly temperature ranges between 1°C in July and 15°C in January. The topography is flat and soils are derived from glacial and volcanic materials, where gravel and stones are commonly found (Paruelo et al. 1988). Average soil organic matter content is very low (<1%) and is heterogeneously distributed (Gonzalez-Polo and Austin 2009).

The vegetation is a mix of tussock grasses and shrubs in a 50% bare soil matrix (Golluscio et al. 1998). The dominant grasses (32% basal cover) are *Stipa speciosa* Trin et Rupr., *Stipa humilis* Cav. and *Poa ligularis* Nees ap., and in lesser proportion, two high-palatable grass species, *Bromus pictus* Hook F and *B. setifolius* Presl. The dominant shrubs (15% basal cover) are *Mulinum spinosum* (Cav.) Pers., *Adesmia volckmannii* Philippi and *Senecio filiginoides* DC (Sala et al. 1989; Golluscio and Oesterheld 2007). Long-term annual aboveground primary production is 56 g m^{-2} $year^{-1}$ (Jobbágy and Sala 2000).

Experimental design

We conducted two field litter decomposition experiments simultaneously over a 3-year incubation period: (1) a soil fauna exclusion experiment; and (2) a fungi reduction experiment. We selected 15 shrubs of *Adesmia volckmannii* of approximately 0.7–1.3 m in diameter and 1 m height within a grazing exclosure established in 1984. We used the shrub microsite because it has shown highest biotic soil activity in the study site (Gonzalez-Polo and Austin 2009). All aboveground herbaceous vegetation was carefully removed below the shrub canopy prior to the beginning of the experiment (January), with an effort to minimize soil disturbance. In order to reduce the photodegradative effects on litter decomposition (Austin and Vivanco 2006), and to homogenize solar radiation interception in all shrub microsites, we covered the soil area below the shrub canopy with a 50% shadecloth, supported by a wire circle of approximately 1.5 m in diameter at 0.2 m above the soil surface. We recognize that this experimental design did not allow for an evaluation of potential interactions between photodegradation and soil faunal decomposition, but our goal was to maintain all microsites with homogenous light conditions simulating a dense shrub canopy in order to avoid confounding effects of variation in plant cover among the treatments.

We constructed litterboxes of 25 × 8 × 1 cm using wire mesh (Blair et al. 1991), with the three different mesh sizes above (10, 2, 0.01 mm mesh) to allow access to macro-meso- and microfauna, respectively (Swift et al. 1979; Bradford et al. 2002). We used a 2-mm mesh below the litterboxes for the 10-mm treatment in order to prevent litter fragments losses but allowing macrofaunal access to the litter (Vossbrinck et al. 1979; Bradford et al. 2002). We placed litter from recently senesced leaves of a native palatable grass species, *Bromus pictus* in the litterboxes, which was collected in the study site and then left air-dried in the laboratory. We chose this palatable species in particular in order to maximize the possibility of detecting soil faunal effects on decomposition. We placed 1.500 g of air-dried litter in each litterbox, loosely tied with a fine copper wire to minimize losses. Each litterbox was transported to and from the field in individual paper bags to minimize litter loss. Any material that remained in the paper bags after transportation was subtracted from the initial litter mass.

The shrub plots were randomly assigned either to control plots, naphthalene addition or fungi reduction treatment ($n = 5$ for each treatment). The soil fauna exclusion experiment (experiment 1) was established using three mesh-sizes litterboxes: (1) 10-mm mesh, which permitted access of all soil fauna (10 mm), (2) 2-mm mesh, which excluded access for macrofauna (2 mm), and (3) 0.01-mm mesh, which excluded access for both macro- and mesofauna (0.01 mm). We placed 6 litterboxes of each mesh size (10, 2 and 0.01 mm) in control and naphthalene plots for a total of 18 litterboxes in each plot. We added a chemical exclusion product (napthalene) on the soil surface below one-third of the shrub plots ($n = 5$), a repellant which has been used in a number of other studies for chemical exclusion of soil arthropods (Yamashita and Takaeda 1998; Green et al. 1999; Heneghan et al. 1999; González and Seastedt 2001; Höfer et al. 2001; Wall et al. 2008; Yang and Chen 2009). Any artifact of mesh-size effect on mass loss could thus be evaluated comparing litter decomposition for the three types of mesh exclusion with and without naphthalene addition.

The fungi reduction experiment (experiment 2) was established with 0.01-mm mesh litterboxes, placed in shrub plots treated with a fungicide (0.01 mm + fungicide). We placed six litterboxes of the 0.01 mm treatment in each fungicide treated plots ($n = 5$), while the 0.01-mm mesh litterboxes in the control shrub plots from experiment 1 functioned as the control treatment for this experiment. All litterboxes (210 in total) were placed in mid-summer (January) on the soil surface and anchored to the soil securely with wire clips.

Naphthalene and fungicide were applied to each of the five shrubs assigned to each treatment at the beginning of the incubation period and then three times a year during 3 years. Naphthalene in crystalline form ("mothballs") was placed on soil surface near the litterboxes at 100 g m^{-2} (Blair et al. 1989), and fungicide (Captan®) was applied on the soil and litterbox surfaces in an aqueous solution (17.5 g m^{-2} dissolved in 3 l of water) (Beare et al. 1992). In order to compensate for any effects of water addition among treatments, the same amount of water was applied to control and naphthalene shrub plots at each time point.

Litterboxes were collected at 4, 9, 12, 16, 24 and 36 months from the beginning of the experiment, transported in paper bags, and placed immediately in an oven for at least 24 h. The litter of each sample was carefully cleaned by removing foreign plant material and soil, and dried in an oven at 60°C for 48 h for dry mass determination. In order to correct the samples for inorganic soil contamination, we estimated initial and final organic matter content with determinations of ash-free dry mass (400°C, 4 h) (Harmon et al. 1999). We estimated the annual rate decay constant (k, $year^{-1}$) using a simple negative exponential model by regressing the logarithm of the fraction of mass remaining against time, using the equation:

$$\ln(M_t/\ M_0)\ = b - kt$$

where M_0 is the initial ash-free dry mass, Mt is the ash-free dry mass at time t, b is the intercept and k (the slope of the function) is the decay constant (Olson 1963). Linear regressions were performed setting the intercept to zero (Vivanco and Austin 2008) and we estimated a decomposition constant (k) for each shrub plot and mesh size. All regressions used to estimate litter mass loss through time were highly significant ($r^2 > 0.90$).

In the fungi reduction experiment, we analyzed litter nitrogen (N) release through time. Litter N concentration at each sampling date (initial included) was determined in both 0.01-mm and 0.01-mm + fungicide treatments by Dumas combustion with a TruSpec® elemental analyzer (LECO, St. Joseph, MI, USA) at the laboratory in the School of Agronomy, University of Buenos Aires. Litter from these fine-mesh treatments had very little soil contamination but were not corrected for possible inclusion of soil N, as total soil N under shrub canopies is less than 0.10% (Gonzalez-Polo and Austin 2009).

Site and litter characterization

During two consecutive years, we took surface soil samples (0–5 cm) in control and fungicide-treated shrub plots. We sieved soils to pass a 2-mm mesh and then a subsample was dried in a 105°C oven for 48 h to determine gravimetric soil water content. Another subsample of 5 g was extracted in the field with 25 ml of KCl 2 N for determinations of inorganic nitrogen. In the laboratory, these samples were filtered and analyzed colorimetrically for NH_4-N and NO_3-N on an Alpkem® autoanalyzer (O–I Analytical, College Station, TX, USA).

To assess the abundance of macrofauna in the site, we placed five pitfall traps (Gist and Crossley 1973) containing a solution of 70% ethylene glycol and 30% alcohol (95 cm^2) for a 5-day period at the end of the first year of incubation (December, late spring) beneath control shrub canopies ($n = 5$). All macrofauna trapped was preserved in the solution, hand picked in the laboratory and then sorted under a magnifying glass (Nikon SMZ 800) to the taxonomic level of order (e.g., Aranae, Hymenoptera, Coleoptera).

The effect of fungicide addition on fungal colonization of litter was tested after 1 year of incubation in the field. Litter subsamples (100 mg) from the 0.01-mm and 0.01-mm + fungicide treatments ($n = 5$) were collected and placed in dilution bottles (falcon tubes) with 2 ml extraction buffer (0.88%. NaCl). Ten-fold dilutions were spread-plated in nutritive agar (potato-dextrose agar, with 50 μg ml^{-1} chlortetracycline and 200 μg ml^{-1} cycloheximide) for determination of fungal coloniziation (Donegan et al. 2001). Plates were incubated at 25°C for 72 h and the colony-forming units (CFUs) were counted.

Statistical analyses

Organic matter remaining (%) at each sampling date, litter decomposition constants (k) and nutrient release data (expressed as percentage of original values) were compared using a one-way ANOVA, as well as data for gravimetric soil water content, and soil NH_4-N and NO_3-N content in control and fungicide shrub plots. Mass loss (%) of years 1, 2, and 3 of incubation for each mesh size were regressed against mass loss (%) of years 1, 2, and 3 for each exclusion treatment (mesh size and chemical exclusion), assuming that any deviations from the 1:1 line could be associated with potential treatments effects (Wall et al. 2008). Independent t tests were performed with equal variances, with the hypothesis that the mesh size and chemical exclusions would only decrease litter mass loss. When necessary, data were transformed to account for the assumptions of the analysis of variance, and a Kruskal–Wallis non-parametric test was used for soil nitrate. Unless otherwise stated, we used 5% for statistical significance; all mean values stated in the text are followed by standard errors in parentheses. We analyzed data with INFOSTAT/Profesional (1.1 Version;

Universidad Nacional de Córdoba, Estadística y Diseño, Argentina).

Results

Effects of exclusion of soil fauna on litter decomposition

Among macrofauna evaluated in the soil surface with the pitfall traps, six taxonomic groups of arthropods were identified (Table 1). Two of the most abundant groups of soil organisms, Coleoptera and Hymenoptera, are known to include litter decomposer organisms (Brussaard 1997), although we did not have the taxonomic resolution to identify them. On average, a total of 3.8 (±0.41) individuals trap^{-1} were found under each shrub, with no evidence of termite presence, and very low number of ants (Hymenoptera, Table 1).

Physical exclusion of macro and mesofauna ('soil fauna' from this point forward) had no effect on litter decomposition. Organic matter remaining (%) was similar among mesh exclusion treatments of 10, 2, and 0.01 mm at all sampling dates (Fig. 1a). On average, between 31 and 33% of the initial litter was decomposed after 3 years of field incubation among all treatments (Fig. 1a). Consequently, litter decomposition constants (k, year^{-1}) did not differ significantly among treatments ($P = 0.36$; Fig. 1b), with average values of 0.14 (±0.009), 0.12 (±0.006) and 0.14 (±0.009) for the 10, 2 and 0.01 mm treatments, respectively (standard error in parentheses).

Chemical exclusion of soil fauna (litterboxes of 10, 2 and 0.01 mm with naphthalene addition) showed no effect on litter decomposition as litter decomposition constants were similar to control treatments without naphthalene addition (Fig. 2). Together, manipulative soil fauna exclusion (either physical or chemical) demonstrated no effect on litter mass loss ($T_{1,34} = 0.04$, $P = 0.51$; Fig. 2).

Table 1 Mean abundance of arthropods (macrofauna) collected in control plots, under shrubs of *Adesmia volckmannii*, where the physical exclusion litterboxes had been placed ($n = 5$)

Taxonomic groups	Individual pitfall^{-1}
Coleoptera[a]	0.6 (0.08)
Diptera	2 (0.15)
Lepidoptera	0.2 (0.04)
Maquilida	0.4 (0.05)
Hymenoptera[a]	0.2 (0.04)
Araneae	0.4 (0.05)
Total	3.8 (0.41)

Standard errors (SE) are in parentheses

[a] Groups containing detritivorous organisms (Brussaard 1997)

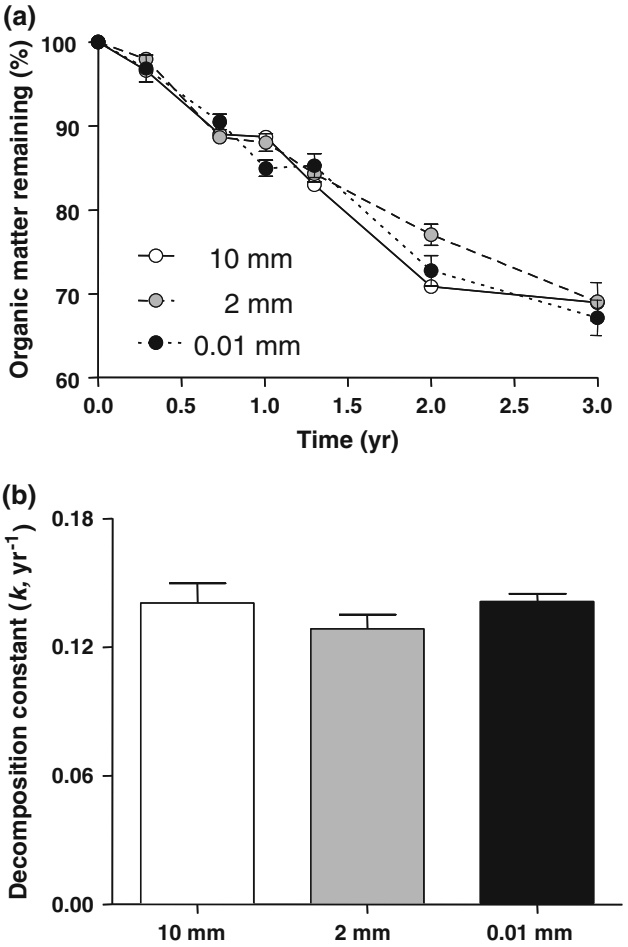

Fig. 1 *Bromus pictus* litter decomposition with physical exclusion of macro and mesofauna. **a** Mean values of organic matter remaining over time (±SE, $n = 5$) for each treatment: no soil fauna exclusion (10 mm mesh, *open circles*); macrofauna exclusion (2-mm mesh, *gray circles*); and macro and mesofauna exclusion (0.01-mm mesh, *black circles*). **b** Mean litter decomposition constants after 3 years (k, year^{-1}) (±SE, $n = 5$) for 10 mm (*open bar*), 2 mm (*gray bar*), and 0.01 mm (*black bar*)

Effects of fungi reduction on litter decomposition and litter nitrogen release

The fungicide application significantly reduced fungal colonization on litter. CFUs from the 0.01 mm + fungicide treatment were significantly lower than in the 0.01 mm (average CFU for fungicide treatment = 20 (±10.6); untreated litter = 219 (±73.8), $F_{1,8} = 16.54$, $P = 0.0036$). Soil water content and soil NH_4-N and NO_3-N content were similar between control and fungicide plots in all sampling dates (Table 2). Mean ammonium concentration in surface soils underneath shrubs for the first year was 3.92 (±1.44) μg g^{-1} dry soil, and mean nitrate concentration was 2.29 (±0.61) μg g^{-1} dry soil ($n = 5$).

Fungi reduction had significant effects on litter decomposition and nitrogen release (Fig. 3). Litter decomposition

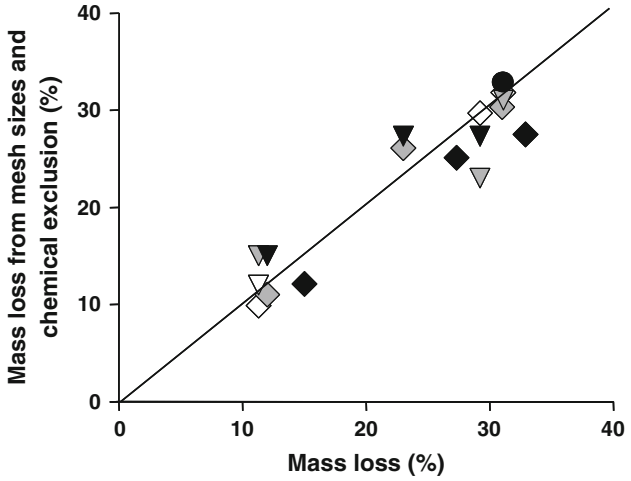

Fig. 2 Comparison of physical and chemical exclusion of soil fauna on litter decomposition in the Patagonian steppe. *Solid line* represents 1:1 relationship either between chemical exclusion and no chemical exclusion treatments, or between different mesh-size exclusion treatments. Chemical exclusion (*diamonds*), physical exclusion (*triangles*); values represent comparisons of treatment means at 1, 2 and 3 years. Different *shading* represents different mesh sizes in both types of exclusion: chemical exclusions effects (10 mm vs. 10 mm + naphthalene, *open diamonds*; 2 mm vs. 2 mm + naphthalene, *gray diamonds*; 0.01 mm vs. 0.01 mm + naphthalene, *black diamonds*); and mesh-size exclusion effects (10 vs. 2 mm, *open triangles*; 10 vs. 0.01 mm, *gray triangles*; 2 vs. 0.01 mm, *black triangles*). No significant exclusion effect was found ($T_{1,34} = 0.04$, $P = 0.51$)

was significantly slowed in the fungicide treatment, with k constants of 0.14 (±0.004) year^{-1} and 0.06 (±0.002) year^{-1}, for the control and fungicide treatments, respectively ($n = 5$). Significant differences in the organic matter remaining (%) between treatments were evident from the second sampling date (Fig. 3a). Only 12% of the initial litter was lost after 3 years of decomposition in the fungicide treatment, whereas 33% was lost in the 0.01 mm treatment (Fig. 3a). Litter decomposing in both fine-mesh treatments immobilized nitrogen during the 3 years of litter decomposition, with stronger immobilization in the 0.01 mm + fungicide treatment, particularly in the second and third years of the incubation (Fig. 3b). Differences in C:N ratios of the decomposing litter also varied over time (Fig. 3c), with a stronger decline in C:N ratios of the 0.01 mm treatment for the first 2 years, which is consistent with increased rates of mass loss in this treatment. However, the immobilization of nitrogen in the 0.01 mm + fungicide treatment continued well into the third year when C:N ratios of both fine mesh exclusion treatments declined (Fig. 3b, c).

Discussion

In this study, we evaluated the contribution of soil organisms on aboveground leaf litter decomposition in the temperate Patagonian steppe, using litterboxes with different mesh sizes and chemical repellents that selectively excluded soil fauna groups. Our results do not provide evidence of an important control of soil fauna in aboveground litter decomposition in this semiarid ecosystem. We found that the physical and chemical exclusion of macro- and mesofauna did not affect litter mass loss and consequently, litter decomposition constants were similar among soil fauna exclusion treatments. However, we found that litter decomposed much more slowly when fungal populations were reduced, suggesting an important role of fungi in aboveground litter decomposition and nutrient dynamics in this semiarid shrub steppe (Fig. 3).

Soil fauna exclusion

The physical and chemical exclusion of macro- and mesofauna did not modify litter mass loss (%) or decomposition constants integrated over the 3-year incubation period (Figs. 1 and 2). Recent studies have demonstrated biome-specific effects of soil fauna on litter decomposition in humid or tropical regions (e.g., Heneghan et al. 1999; González and Seastedt 2001; Höfer et al. 2001; Bradford et al. 2002; Yang and Chen 2009), but strong soil faunal effects were not observed in cold and/or arid ecosystems (Wall et al. 2008). Our results support a minimal role of soil invertebrates on litter decomposition in the semiarid Patagonian steppe, which is in agreement with results from the global experiment of Wall et al. (2008). It appears that the role of soil fauna affecting litter decomposition in arid and semiarid ecosystems may be restricted to particular sites where the combination of faunal community and climate allow for these organisms to flourish, but it does not appear that it is a general characteristic of temperate aridland ecosystems.

The disproportionate role of some macrofauna on litter decomposition may be a particular trait of some warm aridlands, particularly where termite or ant guilds are an abundant component of the soil fauna. In fact, studies in North American and African deserts attribute faster litter decomposition than that predicted by climate indices specifically to termite activity (Santos and Whitford 1981; Schuurman 2005); however, these studies were conducted in warm desert ecosystems where termites are abundant (but see Noble et al. 2009). In contrast, in cold deserts, particularly in the southern hemisphere where temperature could constrain biological activity (Wood 1988) and biogeographic barriers could limit the distribution of termite species, their role as ecosystem engineers may not be prominent, which is consistent with the results of this study.

Considering that we did not find any of the key ‘desert decomposers’ such as termites or ants in our study site, and that the overall macrofauna abundance was relatively low

Table 2 Gravimetric soil water content and inorganic nitrogen concentration in surface soils of control and fungicide plots

	Year 1			Year 2		Year 3
	January	May	October	January	May	January
Soil water (%g H_2O g^{-1} dry soil)						
Control	2.33 (0.45)	6.1 (0.34)	5.92 (0.43)	2.69 (0.25)	4.97 (0.44)	1.3 (0.06)
Fungicide	2.03 (0.1)	5.98 (0.61)	5.75 (0.43)	2.86 (0.27)	6.32 (0.52)	1.47 (0.12)
Soil NH_4-N (μg g^{-1} dry soil)						
Control	6.61 (0.79)	1.69 (0.64)	3.45 (1.03)	3.54 (1.83)	12.11 (5.40)	3.07 (1.52)
Fungicide	6.92 (0.85)	3.72 (0.86)	6.86 (1.82)	9.47 (2.60)	7.36 (3.53)	3.55 (1.85)
Soil NO_3-N (μg g^{-1} dry soil)						
Control	1.06 (0.38)	2.96 (0.51)	2.84 (1.07)	2.17 (0.59)	0.84 (0.42)	0.71 (0.20)
Fungicide	1.20 (0.31)	2.28 (0.38)	0.75 (1.82)	0.95 (0.22)	n.d	0.61 (0.21)

Values represent mean of five plots at each sampling date, with SE in parentheses. Differences between treatments were not statistically significant ($\alpha = 0.05$)

compared to other studies in deserts (Doblas-Miranda et al. 2007) (Table 1), it is reasonable that we observed no response in aboveground litter decomposition to soil macro- and mesofauna exclusion. There are a number of characteristics of the Patagonian steppe that might explain the lack of key macrofaunal decomposers. First, the months of highest rainfall do not coincide with the growing season (Golluscio and Oesterheld 2007) and hence, peaks of resource availability for the soil fauna occur under conditions of low moisture availability. In addition, the asynchrony between water availability and favorable temperatures may constrain the abundance and activity of soil organisms (Heneghan et al. 1999; Schwinning and Sala 2004). Additionally, soil fauna density diminishes with latitude globally (Swift et al. 1979; Heneghan et al. 1999), and deserts are the biomes with the lowest overall soil faunal biomass (Fierer et al. 2009). This combination of climatic and biogeographic factors could explain the absence of soil fauna contribution in aboveground litter decomposition in the semiarid Patagonian steppe when compared to tropical and hot desert ecosystems.

Independent of the effects of faunal exclusion, litter decomposition in this study was lower than others reported in the same study site. Comparing k constants for the same litter incubation period, we reported on average, 0.14 $year^{-1}$ for the control treatment, while average k constants from others studies in the same site ranged from 0.24 to 0.35 $year^{-1}$ (Austin et al. 2006; Austin and Vivanco 2006; Yahdjian et al. 2006). The effects of the shadecloth and shrub canopies in reducing incident solar radiation at the soil surface appears to have had a much larger effect than our soil faunal exclusion treatments, supporting the role of photodegradation as a major control on decomposition in this site (Austin and Vivanco 2006; Austin 2011). These results echo other studies in aridlands suggesting abiotic factors such as solar radiation, wind and freeze–thaw cycles are important controls degrading, fragmenting and redistributing aboveground litter (Moorhead and Reynolds 1989; Gallo et al. 2006; Throop and Archer 2007; Noble et al. 2009; Uselman et al. 2011) rather than a direct biotic control on rates of mass loss. Nevertheless, this experiment did not allow for the evaluation of indirect effects of photodegradation on litter quality, which could potentially interact with soil organisms affecting carbon turnover and litter decay (Gallo et al. 2009; Austin and Ballaré 2010).

Fungi reduction

In contrast with the results for soil faunal exclusion, the role of fungi in biotic degradation of litter is important in the semiarid Patagonian steppe, as originally hypothesized. When fungi were manipulatively reduced, litter decomposed significantly less and with significantly stronger nitrogen immobilization (Fig. 3).

Fungi tolerance to desiccation and the capacity to secrete extracellular enzymes to assimilate several substrates simultaneously (Wilson and Griffin 1975; Whitford and Parker 1989; Austin et al. 2004; Yuste et al. 2010) may explain why litter decomposition was diminished when fungi were reduced. A similar reduction in the magnitude of decomposition was shown in the Chihuahuan desert when fungi were reduced with chemical inhibitors (Santos and Whitford 1981; Parker et al. 1984; Whitford et al. 1986). In this study, it is not clear whether the reduction in fungal abundance changed bacterial populations or other microfloral and microfaunal groups, although we did not observe any compensatory microbial responses which resulted in positive effects on rates of mass loss in litter from fungicide-treated plots. We were not able to evaluate

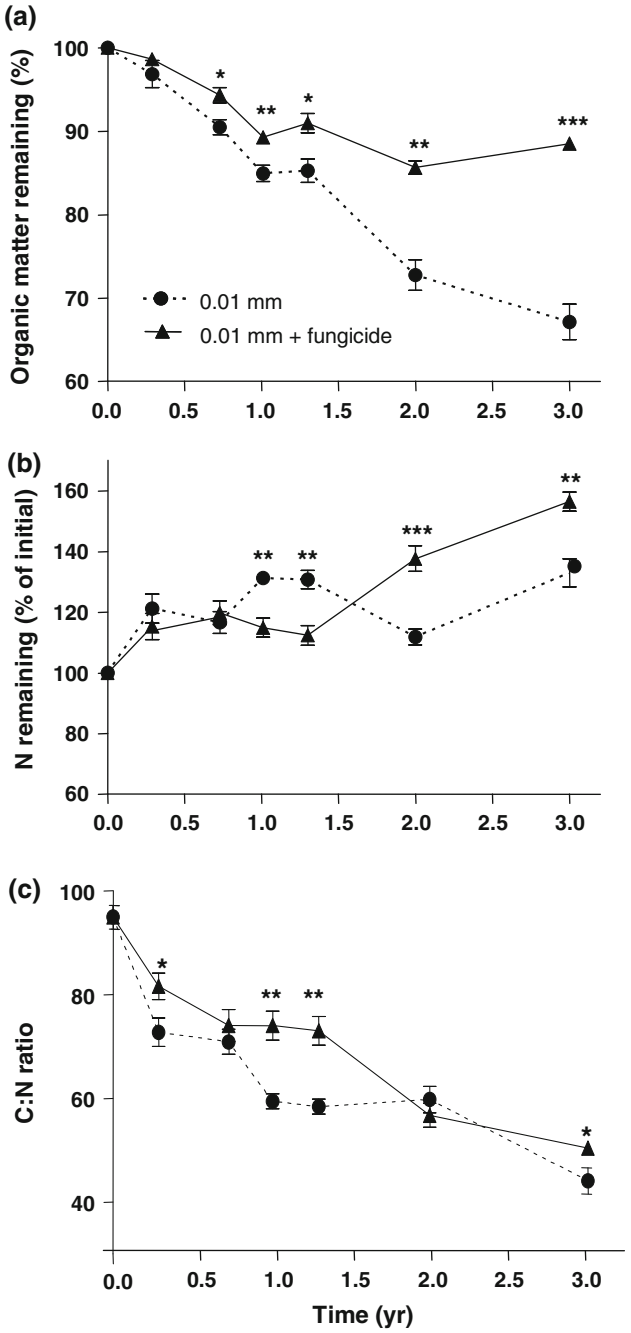

Fig. 3 Microbial decomposition of litter of *Bromus pictus* and N release with reduction of soil fungi. **a** Mean organic matter remaining over time, (%, ±SE, $n = 5$) at each time point: macro-and mesofauna exlusion (0.01 mm, *filled circles*) and fungi reduction (0.01 mm + fungicide, *filled triangles*); **b** Mean nitrogen remaining (% of initial N, ±SE, $n = 5$) over time. **c** C:N ratios over time (±SE, $n = 5$). Significant differences between treatments are noted ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$)

the potential fungi reduction–soil organism interactions, which have been shown to be important in affecting soil faunal dynamics in warm desert ecosystems (Parker et al. 1984) and could be particularly important when termites are abundant (Schuurman 2005). Overall, the strong reduction in decomposition appears to arise from the direct impact on fungal populations and their controls on carbon turnover in this ecosystem.

Net nitrogen immobilization was observed over time in both treatments (Fig. 3b), but a stronger immobilization occurred in the fungicide treatments and continued over the entire incubation period. The C:N ratios tracked mass loss changes during the first 2 years of the experiment, suggesting that decreased C:N ratios could be explained in part by loss of carbon from decomposition. Additionally, the differences in nitrogen immoblization between the two treatments could stem from stoichiometric constraints on different microbial groups such as fungi or bacteria (Manzoni et al. 2008). In other experiments in the Patagonian steppe, where litterbags were placed in bare soil microsites, litter nitrogen immobilization was very low (Yahdjian et al. 2006) or non-existent (Austin et al. 2006). The results from this study support the assertion that the area beneath shrubs is a hotspot for biotic activity in this ecosystem, as opposed to bare soil areas where abiotic controls dominate (Gonzalez-Polo and Austin 2009).

Although soil fauna have been mentioned as a key control of litter decomposition in some aridlands, our results highlight that this could not be generalized globally to all arid and semiarid ecosystems. Alternatively, although we did not observe any effect of soil fauna on aboveground litter decomposition, soil organisms may be critical belowground (Collins et al. 2008) while position of litter, aboveground or buried, could be critical in determining the principal controls on mass loss (Austin et al. 2009). In addition, the contribution of soil fauna to litter decomposition appear to depend on site-specific factors, such as faunal richness and abundance (Wall et al. 2008) which in turn may be influenced by factors such as soil fertility, trophic interactions and evolutionary history (Powers et al. 2009).

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Conflict of interest None.

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