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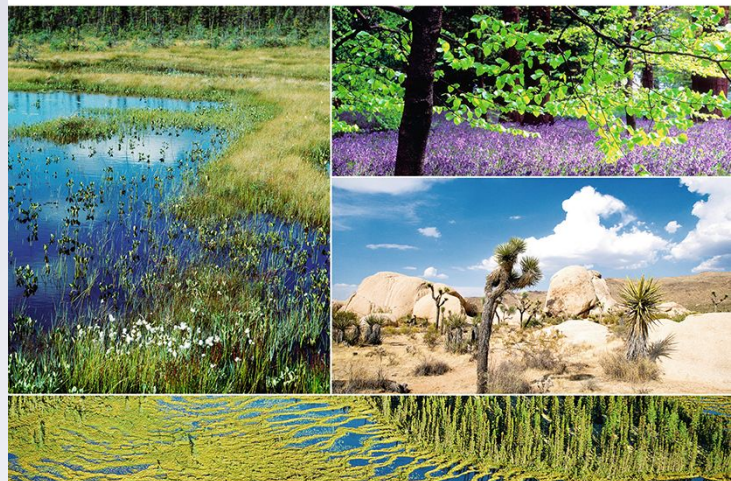
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# Increased litter decomposition rates of exotic invasive species *Hieracium pilosella* (Asteraceae) in Southern Patagonia, Argentina

Karen Braun · M. B. Collantes · L. Yahdjian · C. Escartin · J. A. Anchorena

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**Abstract** Plant invasions can affect key ecosystem processes regulating carbon and nutrient balances, i.e., litter decomposition. Exotic herb *Hieracium pilosella* (hawkweed, Asteraceae) recently invaded steppes of Tierra del Fuego island, Southern Patagonia, Argentina, where plant communities exhibit different vulnerabilities to invasion. To investigate *H. pilosella* invasion's effects on litter decomposition, we conducted a field experiment in two plant communities, a tussock grassland and a grazing lawn, having contrasting environmental conditions and different vulnerabilities of being invaded by *H. pilosella*. At each community, we decomposed litter of dominant native species and of the exotic herb during 24 months. In addition, we characterized the litter qualities of the different species, and the microclimates of the communities. Exotic litter decomposition was remarkably faster and showed a higher association to

microenvironmental variability compared to native litter decomposition. *H. pilosella* decomposed three-times faster than native litter in the moister, and more susceptible to invasion by *H. pilosella* plant community, the tussock grassland. By contrast, decomposition of native litter was not associated to the contrasting environmental conditions of the studied communities. Results suggest that introduced species may exhibit different ecosystem process rates and controls compared to resident species, affecting ecosystem nutrient and carbon cycles.

**Keywords** Carbon cycle · Grasslands · Litter decomposition · Ecosystem process · Plant invasions

## Abbreviations

VPD Vapor pressure deficit

MAP Mean annual precipitation

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## Introduction

Litter decomposition is a key process in terrestrial ecosystems, providing the most important source of nutrients for plants and soil organisms, and regulating CO<sub>2</sub> release to the atmosphere (Raich and Schlesinger 1992). Main factors controlling this ecosystem process are temperature (Meentemeyer 1978), moisture, the litter chemical quality, i.e., C/N, lignin/N ratios (Melillo et al. 1982), and the litter decomposing

community (Swift et al. 1979). Due to the current interest in controlling rising atmospheric carbon dioxide concentrations and the large extent of biological invasions, understanding the effects of exotic species invasions on the litter decomposition process has become crucial.

Litter quality is known to affect the decomposers biological activity and the litter decomposition rates (Talbot and Treseder 2012), thus, invasions by plant species having a different litter quality compared to native species may strongly affect litter decomposition rates (Ehrenfeld 2003; Spirito et al. 2014). In a meta-analysis of 94 studies on plant invasions, Liao et al. (2008) found higher litter decomposition rates of invasive plants native, apparently explained by their higher litter N concentration compared to native species. Godoy et al. (2010), in turn, found lower decomposition rates of invasive species compared with their native counterpart analyzing 19 pairs of co-familial native and invasive species, apparently explained by the invasive litter higher lignin content.

Northern steppes of Tierra del Fuego island, Argentina, dominated by harsh-cuticled shrubs and grasses adapted to arid conditions, were recently (around 20 years ago) invaded by the exotic herb *Hieracium pilosella* (Asteraceae) (Livraghi et al. 1998), a soft-tissued rosette herb native from Europe and West Asia (Bishop and Davy 1994). This herb is a known invader of grasslands in many countries, like New Zealand (Treskonova 1991), the UAS (Vander Kloet 1978), Switzerland (Winkler & Stöcklin 2002) and Chile (Covacevich 2009). Studies in New Zealand have reported that *H. pilosella* invasion has affected the carbon cycle; since the soil at invaded patches had a lower C/N ratio, higher organic N, higher CO<sub>2</sub> respiration (Saggar et al. 1999), and higher organic C (McIntosh et al. 1995) compared with the soil with indigenous vegetation. Cipriotti et al. (2010) found that *H. pilosella* quickly spread along Tierra del Fuego island northern steppe ecosystems (ca 5000 km<sup>2</sup>) by means of wind-carried seeds, forming large monospecific “carpets” (sensu Scott et al. 2001) replacing native flora in highly disturbed sites (Cipriotti et al. 2010). This exotic species’ colonization success in the fuegian steppe has been associated to soil disturbance and to plant community, with steppe plant communities having different susceptibilities to being invaded by *H. pilosella* (Rauber et al. 2014, 2016). Tussock grasslands are more invaded

than the grazing lawns (Cipriotti et al. 2010), apparently due to a higher moisture availability in the tussock grasslands (Rauber et al. 2013) and not to plant community biotic constraints (Rauber et al. 2013, 2014). Braun et al.’s (2010) phyllogeographic studies on *Hieracium* genera in Southern Patagonia showed no hybridization among exotic and native species of the genera; and a very low geographical genetic variability of *H. pilosella*, suggesting reproduction by means of apomictic seeds. Cipriotti et al. (2012) found that at local scales, the application of selective herbicides (broad leaf), combined with fertilizers and with a transient sheep grazing exclusion, enhances native grasses’ regrowth. Recommended management strategies are domestic cattle management to avoid overgrazing, the minimization of soil massive disturbances and tillage, and the quick restoration of areas having bare soil (Braun et al. 2010).

Previous research on *H. pilosella* invasion in Tierra del Fuego, summarized in Cipriotti et al. (2018), have extensively investigated *H. pilosella* invasion and the related land-use and ecological factors, and proposed management tools on the invasion. *H. pilosella* invasion ecosystem effects, i.e., on the soil carbon storage and fluxes, have been reported for other systems (Saggar et al. 1999); however, underlying mechanisms are poorly known. Differences in key traits like leaf tissue between invader and resident species are known to determine exotic species invasion ecosystem effects (Levine et al. 2003). *H. pilosella* soft tissue suggests a less-lignified litter compared to the aridity-adapted lignified cuticles (Coughenour 1985) of the native litter; a trait known to affect litter decomposition rates (Melillo et al. 1982; Talbot and Treseder 2012). In addition, Conant et al (2008) found experimentally that the decomposition of recalcitrant litter exhibited a higher response or sensitivity to warming compared to labile litter decomposition, suggesting that substrate quality may affect decomposition sensitivity to environmental factors. Litter decomposition rates of *H. pilosella* and their sensitivities to abiotic factors compared to native litter have not been explored so far. We hypothesize that *H. pilosella* litter is more labile than the litter of native-dominant species, and thus this exotic species litter will decompose faster and will exhibit a different interaction with the microenvironment compared to litter decomposition of the native-

dominant species. To test these hypotheses, we established a litter decomposition field experiment to estimate litter decomposition rates of the invading herb *H. pilosella* and of the native-dominant species in two noninvaded plant communities having contrasting environmental conditions and vulnerabilities to invasion by *H. pilosella* or invasibility, a tussock grassland and a lawn. In addition, we characterized the initial litter quality and the microclimates of the studied communities, and we analyzed the relationship of litter decomposition and plant community's vulnerability to invasion by *H. pilosella*.

## Materials and methods

### Study site

The experiment was set in the María Behety Ranch (350 mm mean annual precipitations), located close to Río Grande city (53°47'27"S, 67°42'46"W), in the center of the steppe area of Tierra del Fuego Island. The Fuegian steppe occupies northern Tierra del Fuego Island, Argentina, covering about 5.000 km<sup>2</sup>, from the Magellan strait in the north to ca. 54°S. The weather is cold-oceanic; with 10 °C mean temperature in summer and 0 °C in winter, with precipitations evenly distributed along the year (MAP 361.8 mm). During the summer, there is a water deficit (Walter and Box 1983) due to the high evaporation rates produced by the strong winds (Korembliit and Forte Lay 1991). The main land use of the region after European settlement during the last decade of the nineteenth century has been extensive sheep grazing (0.8 sheep ha<sup>-1</sup> all year round) to produce wool and meat (Cingolani et al. 1998). The vegetation has been classified as a humid grass steppe (León et al. 1998; Collantes et al. 1999); controlled by topography and soil nutrient gradients (Collantes et al. 1999). Tussock grasslands cover undulated plains located at not-Northern aspects, having loamy, slightly acidic soils, and having tall and structurally complex vegetation dominated or co-dominated by the tussock grass *Festuca gracillima* and/or by the shrub *Chiliodriscum diffusum*, both interspersed in a matrix of soft grasses (mostly *Festuca magellanica*, *Avenella flexuosa*, *Poa spiciformis*, *Poa pratensis*, and *Hordeum pubiflorum*) and forbs. Grazing lawns, hereafter lawns, occur mainly at steep (60%) Northern hill aspects (warmer

than the Southern aspects in the Southern hemisphere) highly exposed to wind and sun, having fine-textured, base-rich soils, and a short and open vegetation structure (Posse et al. 2000) dominated by soft grasses (*Hordeum pubiflorum*, *Poa pratensis*, *Festuca magellanica*). Lawns exhibit a reduced leaching due to soil compaction by severe trampling, and a high nutrient input due to sheep overgrazing in the past (Collantes et al. 1999). Apart from *H. pilosella*, few exotic species have been reported in the area, being the more conspicuous *Taraxacum officinale*, *Veronica serpyllifolia*, and the cosmopolitan grass *Poa pratensis*. However, those species have not become dominant nor did they show an increase in response to domestic grazing. *Poa pratensis*, in particular, has become naturalized and is not considered an ecological problem (Collantes and Anchorena 1993; Collantes et al. 1999).

### Experimental design

We performed a two-factor (species and plant community) field experiment to compare exotic and native or resident (hereafter native) litter decomposition rates in two plant communities, a tussock grassland and a lawn (Cipriotti et al. 2010). The experiment was set in two enclosures, one set at a lawn community and another at tussock grassland. Table 1 shows initial soil parameters of the studied communities. The experimental sites were not invaded by *H. pilosella*. In addition, we characterized the chemical parameters of the different substrates, and we measured the microclimate of the studied communities simultaneously to the experiment. Soils of the studied plant communities had relatively high nutrient availability, as indicated by their base content and C/N ratios. However the lawn had neutral soil characteristics according to the pH and the cation exchange capacity, and exhibited higher base saturation, while the soil of the tussock grassland was slightly acid, with a higher total carbon content and lower base saturation (Table 1).

We estimated decomposition rates of three litter identities (hereafter Species), invading exotic herb *H. pilosella*; soft grasses (mixture of plant species); and tussock grass (*Festuca gracillima*) in two plant communities, a tussock grassland and a lawn, resulting in six treatments (3 species × 2 plant communities). Standing dead biomass of the different litter identities was field-collected at the beginning of the spring, air-

**Table 1** Soil chemical parameters measured in composite samples of the upper horizon (5–15 cm) of the studied plant communities following Jackson (1981) methodology for all parameters, except Total N (Kjeldahl, modified by Ritcher 1980)

pH (H <sub>2</sub> O)	Electric conductivity	Total C (g/kg)	Total N (g/kg)	P (ppm)	Cation exchange capacity (meq/100 g)	Ca	Mg	Na	K	Base saturation (%)
5.8	0.047	96.64	7	8.6	59.3	21.2	6.3	0.7	4.2	0.546
7.4	NA	32.5	3.22	2.2	22.99	16.4	4.8	0.5	1.2	0.996

dried in the laboratory, weighted to 2 g and placed in the litter bags. The soft grasses litter was collected in a lawn, where it is the dominant group of species, and was composed by a mixture of native (*Hordeum pubiflorum*, and *Festuca magellanica*) and naturalized (*Poa pratensis*) species in the same proportion that they are found in the plant community. The tussock grass (*F. gracillima*) litter was collected in the tussock grassland, where it is the dominant species. The litter from *H. pilosella* was collected in an invaded area close to the study site.

We estimated litter decomposition rates ( $k$ ) ( $\text{year}^{-1}$ ), which describe the rate of organic mass loss over time, using the litterbag technique, in which a litter is confined in a bag, incubated in the field, and recovered at periodic intervals to estimate organic mass loss (Singh and Gupta 1977). Using this methodology, each bag is recovered and processed only one time, one measurement being independent of the other. We used 15 × 15 cm litter bags made of 2-mm mesh sized fiberglass, a mesh-size large enough to allow access to most decomposer fauna (Robertson and Paul 2000). The subsamples of the different litter identities were stove dried (70 °C for 72 h) to calculate the initial moisture content of the air-dried litter. Also, we determined initial values of ash-free dry mass by muffle furnace calcination (4 h at 500 °C) for each species.

At each plant community, we set six experimental plots (Fig. 1) where we placed litterbags anchored with metal pins on the soil surface at the end of December (summer in the Southern Hemisphere). The litterbags were randomly collected at four dates corresponding to 2, 13, 15, and 24 months of incubation. We employed 3 replicates per treatment (combination of Plant community and Species), and date, resulting in a total of 432 litter bags (3 replicates × 6 plots × 4 dates × 2 plant communities × 3 species). After field collection the litter bags were returned to

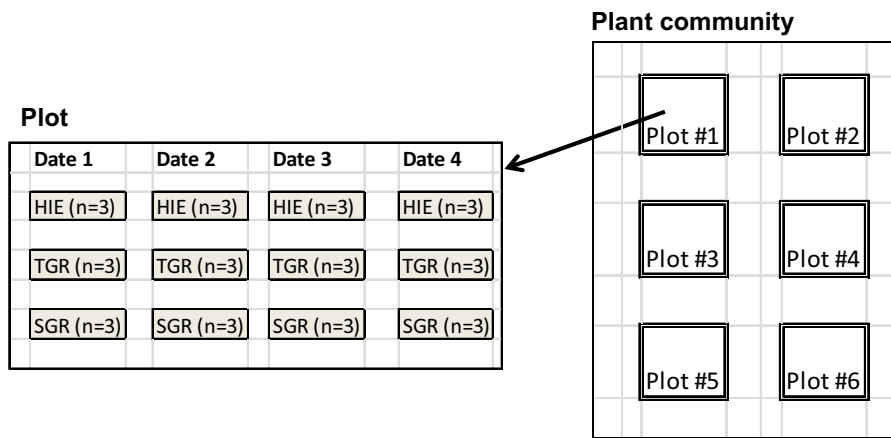
the laboratory where their content was carefully cleaned by hand discarding foreign material from the litter (lichens, plants, soil) and stove-dried at 70 °C until constant weight, and weighted. Ash-free dry mass was determined on subsamples of ground material by muffle furnace calcination (4 h at 500 °C) to correct for soil contamination from the field (Harmon et al. 1999).

#### Initial litter-quality characterization

To characterize the initial litter quality, we determined total N by the micro-Kjeldahl method ( $n = 5$ ); and soluble compounds, hemicelluloses, cellulose, and lignin concentration by successive extractions with acid-detergent reactions ( $n = 5$ ) (Van Soest 1963). Using these litter chemical parameters, we calculated standard litter-quality indexes, i.e., lignin/N, C/N, cellulose/N, and cellulose + hemicelluloses (Melillo et al. 1982; Taylor et al. 1989).

#### Microclimate characterization

To characterize the microclimate of the studied communities, we measured air temperature (°C), luminosity ( $\text{lum}/\text{ft}^2$ ), and relative humidity (%) using the sensors connected to four mini data-loggers (HOBOS) placed on the soil surface at each of the plant communities (two at each plant community). All measurements were taken in the air, close to the soil surface. The mini data-loggers were placed in areas nearby the study plots where the vegetation was not disturbed by the experiment. The microclimatic data were recorded hourly every day during one month in each season (February, April, July, and October). From the hourly measurements of each day (24), we extracted the daily maximum and minimum temperatures, maximum luminosity, and calculated the total daily luminosity. Also, from the hourly measurements



**Fig. 1** Experimental design. Scheme of the experimental design showing the six plots set at each of the two plant communities studied (tussock grassland and lawn, 12 plots in

total), and the detail of the litterbags with the different species identities (TGR: tussock grass, SGR: soft grass, HIE: *Hieracium pilosella*) set at each plot

of relative humidity of each day (24), we calculated the vapor pressure deficit (VPD), and then we extracted the daily maximum VPD (KPa).

#### Data analysis

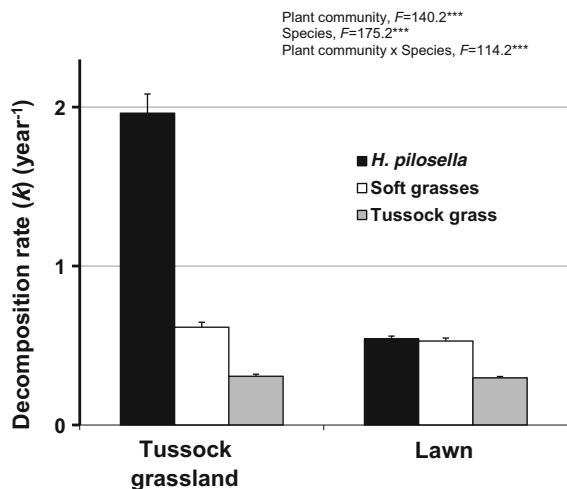
We fitted litter remaining ash-free dry matter along time to a negative exponential model, in which  $k$  (decomposition constant or speed of organic mass loss) ( $\text{year}^{-1}$ ) was estimated by regressing the natural log of the fraction of organic matter remaining against time (exponential model  $M_t/M_0 = e^{-kt}$ , where  $M_t$  = remaining mass after a period of time,  $M_0$  = initial mass) (Olson 1963).  $k$  was independently estimated for each plot and treatment ( $n = 6$ ) to enable statistical comparisons. Replicates of mass-loss values per plot ( $n = 3$ ) were averaged to obtain one single value per treatment per date. Linear regressions were performed setting the intercept to zero.

To study litter origin's (native or exotic) effect on decomposition rates ( $k$ ) and its interaction with plant community, we grouped tussock grass and soft grasses in "native litter" and performed a two-way ANOVA (litter origin and plant community). Species' and plant community's effects on litter decomposition rates ( $k$ ) and their interactions were analyzed with a two-way ANOVA. To compare litter decomposition dynamics in times of the different species in the two plant communities studied, we performed a three-way ANOVA, using time, species, and plant community as factors, and organic matter remaining (percentage of

the initial) at each date for each species as a response variable. In addition, differences in organic mass loss at each date for the different species were analyzed with a one-way ANOVA followed by post hoc comparisons. Differences in initial litter quality between species were assessed with one-way ANOVA, and the same analysis was used to study differences in microclimatic parameters between plant communities. All post hoc comparisons were performed with a Tukey test, and an  $\alpha$  of 5% was used for all the statistical analyses. Data fulfilments of the assumptions of the tests were checked before performing the analysis. Statistical analyses were performed using the SPSS package 11.4 (Chicago, Illinois).

#### Results

Litter origin, i.e., native or exotic, had a strong effect on litter decomposition rates ( $k$ ) obtained ( $F_{1,35} = 181.1$ ,  $p < 0.0001$ ), which interacted with the plant community ( $F_{1,35} = 128.3$ ,  $p < 0.0001$ ). The litter decomposition rate ( $k$ ) obtained for the invading herb *H. pilosella* incubated at the tussock grassland, the more susceptible-to-invasion plant community, was three times higher than the higher decomposition rate obtained for the native species in this study ( $k = 1.96 \pm 0.12 \text{ year}^{-1}$  vs.  $k = 0.62 \pm 0.03 \text{ year}^{-1}$ , respectively, Fig. 2). By contrast, *H. pilosella* litter decomposed at a similar rate as the litter of the soft

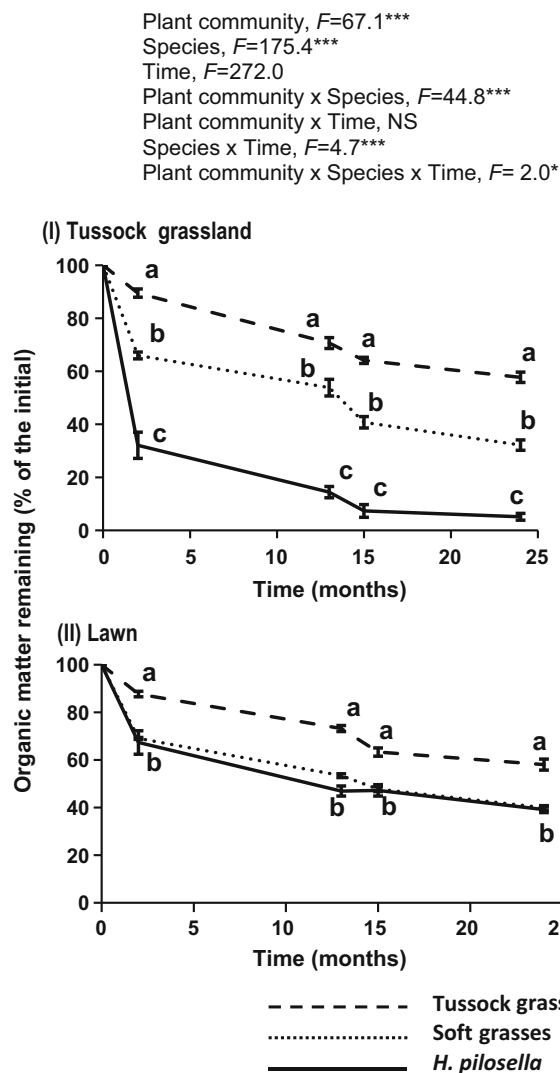


**Fig. 2** Decomposition of native-dominant litter (soft grasses and tussock grass *F. gracillima*) and of the invader herb *H. pilosella* in intact (noninvaded) tussock grassland and lawn plant communities (high and low invasibility by *H. pilosella*, respectively). Bars are mean + 1 SE of decomposition rates,  $K$  (year<sup>-1</sup>) ( $n = 6$ ) obtained after a 2-year litterbag incubation. Fisher parameters ( $F$ ) are from the two-way (plant community and species) ANOVA, \*\*\*  $p < 0.001$

grasses at the less-invasible plant community, the lawn (Fig. 2). Plant community's effect was remarkable for *H. pilosella* litter decomposition rates, which was almost four times faster at the tussock grassland compared with the lawn (Fig. 2). On the contrary, native species decomposed at similar rates at both plant communities, and the litter of the soft grasses decomposed significantly faster than the litter of the tussock grasses (Fig. 2).

Organic matter loss dynamics analysis showed that differences among species in litter decomposition were observed both at the tussock grassland ( $F_{2,35} = 182.3$ ,  $p < 0.001$ ) and at the lawn ( $F_{2,35} = 63.7$ ,  $p < 0.001$ ) from the beginning of the experiment (Fig. 3). In fact, during the first two months of incubation, *H. pilosella* litter lost around the 68% of organic matter in the tussock grassland, while the litter of native species at both plant communities and of *H. pilosella* at the lawn lost between 10 and 30% of organic matter (Fig. 3).

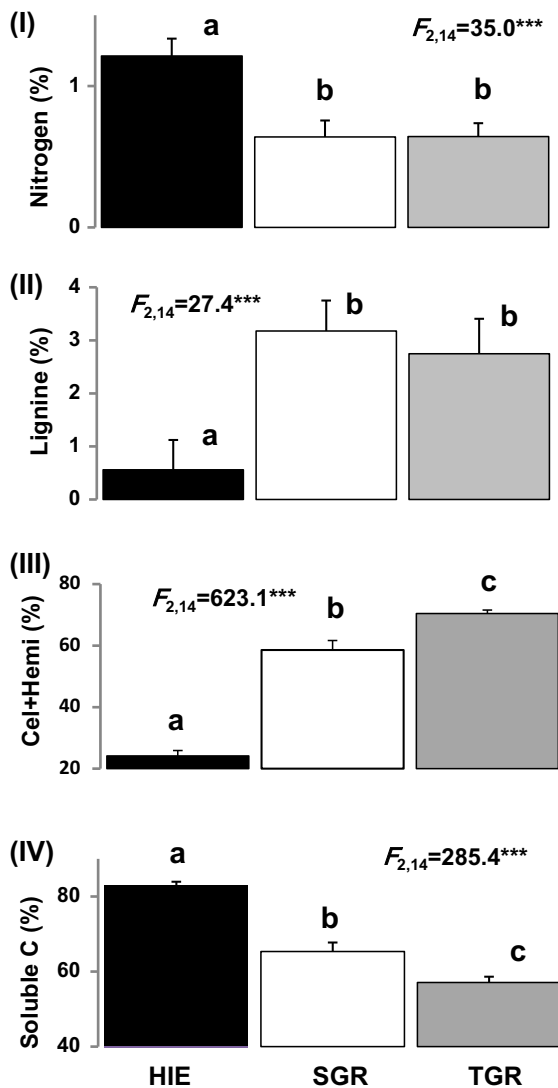
The litter quality of the exotic herb *H. pilosella* was remarkably different from the litter of native species (Fig. 4). *H. pilosella* had higher concentrations of labile compounds, i.e., N and soluble C, and a lower concentrations of recalcitrant substances, i.e., lignin, cellulose + hemicelluloses, compared with the litter



**Fig. 3** Organic matter remaining (percentage of the initial) through time of litter of native-dominant species (soft grasses and tussock grass *F. gracillima*) and of the invader herb *H. pilosella* during a two-year field litterbag incubation in the tussock grassland (I) and in the lawn (II). Points are the mean ± 1 SE of organic matter remaining (%) in each collection date ( $n = 6$ ). Different letters show significant differences between litter identities at each date according to a one-way ANOVA ( $p < 0.001$ ) followed by Tukey contrasts. Fisher parameters ( $F$ ) correspond to a three factor ANOVA (time, species and plant community) \*\*\*  $p < 0.001$

of native species (Fig. 4). Native species differed among them in their litter quality by a much lesser extent; with soft grasses having more soluble C and less cellulose and hemicelluloses than the tussock grasses (Fig. 4). The tussock grassland and the lawn had contrasting microclimates. The lawn was higher





**Fig. 4** Initial litter qualities of the invading species *H. pilosella* (HIE, dark bar) and of the native-dominant species (soft grasses, SGR, white bar; and tussock grass (*F. gracillima*), TGR, gray bar). (I) Nitrogen content (%), (II) Lignine content (%), (III) Cellulose + hemicelluloses (%), (IV) Soluble carbon content (%). Bars are mean + 1 SE ( $n = 5$ ). Different letters show significant differences according to the one-way ANOVA followed by Tukey contrasts. \*\*\*  $p < 0.001$

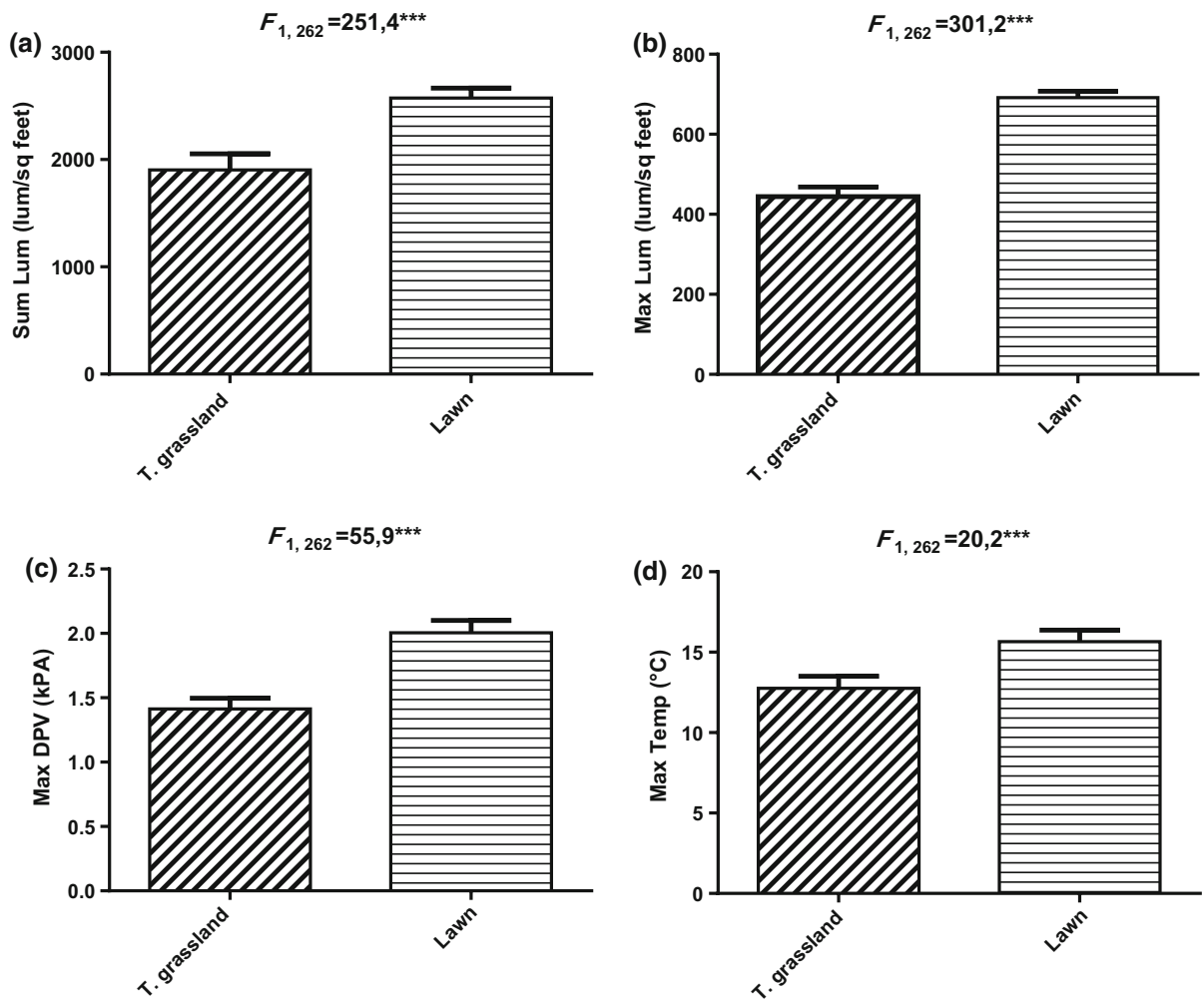
daily maximum temperatures (Fig. 5a), more insulated (daily maximum and sum of luminosity, Fig. 5c, d), and drier (higher daily maximum VPD) (Fig. 5b) compared to the tussock grassland. The plant communities did not differ in their daily minimum temperatures (data not shown).

## DISCUSSION

Litter of the invading herb *H. pilosella* was more labile and decomposed significantly faster than the litter of native species at the tussock grassland, the cooler, moister and more vulnerable to invasion-by-*H. pilosella* plant community (Cipriotti et al. 2010). By contrast, native litter decomposition was modestly or not associated at all to the great microenvironmental variability found (Fig. 5).

Decomposition rates of the native litter ranged from 0.31 to 0.62 year<sup>-1</sup>, being similar to reported rates of other dominant species of the steppe, i.e., the scrub *Chiliotrichum diffusum* (0.53 ± 0.03 year<sup>-1</sup>) (Braun 2009), and within the values obtained for high (higher than 50°) latitude sites having similar temperatures and annual precipitation as northern Tierra del Fuego island (Zhang et al. 2008). Soft grasses litter decomposed faster than tussock grass litter at both communities (Fig. 2), probably explained by their higher litter quality or because litter mixes may result in increased decomposition rates (Vivanco and Austin 2008). By contrast, the exotic herb *H. pilosella* decomposed at a rate close to 2 year<sup>-1</sup> at the tussock grassland, a decomposition rate estimated for mid-latitudes sites, with mean annual temperatures higher than 15 °C (Zhang et al. 2008). This result is in accordance with other studies that reported faster decomposition rates for invading species having a more labile litter, i.e., litter with higher nutrient concentration (Allison and Vitousek 2004; Ashton et al. 2005) or higher specific leaf area (SLA) (Castro-Díez et al. 2009) compared to native species.

Litter decomposition of the studied species was highly associated to litter quality; in agreement with studies comparing decomposition rates within biomes worldwide (Cornwell et al. 2008). Despite the remarkable microclimatic differences of the studied plant communities, i.e., cool and moist conditions at the tussock grassland compared to the more insulated and dry lawn (Fig. 5), native litter decomposition was similar at both of them. By contrast, *H. pilosella* litter decomposed faster at the moister plant community, the tussock grassland, as expected for a semiarid ecosystem with water availability constraints (Risch et al. 2007; Yahdjian et al. 2006). Results suggest different responses to microenvironmental variability of exotic and native litter decomposition, which may be associated to their contrasting quality (Conant et al. 2008;



**Fig. 5** Microclimatic parameters of the tussock grassland (T. grassland) and the lawn. Bars are mean + 1 SE ( $n = 132$ ) of **a** Daily sum of luminosity (Sum Lum); **b** Daily maximum luminosity (Max Lum); **c** Daily maximum Vapor Pressure

Deficit (Max VPD); and **d** Daily maximum temperature (Max Temp). Data were recorded hourly every day during one month in each annual season. Fisher parameters ( $F$ ) are from the one-way (plant community) ANOVA,  $*** p < 0.001$

Fierer et al. 2005). Adaptations of native species to the semiarid conditions of the steppe result in harsh-lignified cuticles (Coughenour 1985), leading to the complex-recalcitrant tissues we found (Fig. 4). The litter of *H. pilosella*, on the contrary, has a particularly high nutrient content, but also a high soluble C content, also called high-quality C, formed by small symmetrical and mostly intracellular C compounds, i.e., some sugars, easily degraded by microorganisms (Waldrop and Firestone 2004). In addition, the great abundance of hairs in the cuticle of *H. pilosella* leaves (absent in native species), may capture water and

create a more humid microenvironment on the leaves surface, favoring the biotic activity (Braun 2009).

Litter decomposition in arid and semiarid lands has been described as an abiotically driven process, controlled by litter physical fragmentation by wind, rain or sun (Cepeda-Pizarro and Whitford 1990; Moorhead and Reynolds 1989; Montaña et al. 1988); or due to photodegradation, as described for northern Patagonia (Austin and Vivanco 2006). In our studied system, physical fragmentation or photodegradation should have led to higher decomposition rates in the warmer, drier and more insolated community, i.e., the

lawn. Also, moisture enhancement of *H. pilosella* litter decomposition in the tussock grassland suggests an increase of microdecomposers biomass and activity triggered by humidity (Schimel et al. 1999). Both results, i.e., the lack of warming or insolation effects and the moisture effect on litter decomposition rates, suggest a lack of litter physical weathering and a biologically driven decomposition process. The oceanic weather of Tierra del Fuego steppe (Koremlit and Forte Lay 1991) determines less arid conditions compared with continental ecosystems having a similar MAP, and may account for the apparent higher microbial activity. The relative importance of soil biota in the decomposition process (González and Seastedt 2001) has been globally related to climatic factors (Wall 2008), aridity in particular (Couteaux et al. 1995).

Conclusions drawn from experiments in arid or semiarid lands or in common garden experiments using native-recalcitrant litter (e.g., Cepeda-Pizarro and Whitford 1990; Austin et al. 2009) may underestimate both biotic factors and litter-quality effects on decomposition. In the same vein, a positive interaction among a species' decomposition at a particular site, i.e., *H. pilosella* decomposing in the tussock grassland, does not necessarily imply the specialization of the decomposer biota for a species, also called "affinity effect." In our field experiment, litter of *H. pilosella* was transplanted into noninvaded plant communities, thus, no adaptation or specialization of the decomposer organisms could have taken place.

Increased litter decomposition rates of *H. pilosella* in the tussock grasslands, the plant community more susceptible of being invaded compared to the lawn (Cipriotti et al. 2010; Rauber 2011; Rauber et al. 2016), may result in higher soil nutrient availability compared to noninvaded communities, as it has been reported for sites invaded by *H. pilosella* in New Zealand (Saggar et al. 1999). Steppe plant communities with high soil nutrient availability are more suitable for *H. pilosella* invasion (Rauber 2011; Rauber et al. 2016). Thus, this exotic species colonization may alter the environment in a way to create conditions favorable to its own invasion. Positive feedbacks between exotic species invasion and ecosystem functioning effects and have been reported for other invading species (Suding et al. 2004; Vitousek et al. 1987). For example, the invasion of *Tradescantia fluminensis* in New Zealand determined

increased decomposition rates at invaded sites, transforming the podocarp forest ground originally covered by litter into tall and dense mats of the invasive species (Standish et al. 2004). Also, the invasions by N-fixing trees in Hawaii volcanic landscapes (Vitousek et al. 1987; Vitousek and Walker 1989) or in South African scrublands (Yelenik et al. 2004) resulted in increased soil N availability, favoring secondary weed invasion and impairing native species recolonization.

Finally, our results reveal complex interactions between litter decomposition rates, litter quality, microenvironmental variability, and plant communities' susceptibility to invasion, and suggest that introduced species may interact differently with the environment compared with native species, affecting ecosystem process. Decomposition controls described for grasslands are complex and have contrasting patterns (Epstein et al. 2002; Yahdjian et al. 2006) differing from global scale controls, i.e., temperature (Bontti et al. 2009). Invasive herb *H. pilosella* higher litter decomposition rates compared to native litter may result at invaded sites in increased CO<sub>2</sub> release to the atmosphere, main gas responsible of the global warming, and in a decrease of the soil C storage (Couteaux et al. 1995). However, the litter of this exotic species can interact with the litter of other species through mixed synergic or antagonistic mechanisms (Chapman and Koch 2007; Gartner and Cardon 2004); and C inputs to the system by means of net primary production (Couteaux et al. 1995) may also be affected by the *H. pilosella* invasion; facts that should be explored in further studies to determine the impact of this invasion on the system C balances.

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