



Original article

Scaling-up from species to ecosystems: How close can we get to actual decomposition?



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ABSTRACT

Predicting global changes and their effects on ecosystem functioning has been a central issue of ecology during the last decades. Scaling-up from species characteristics to ecosystem processes is a common approach to achieve that goal. However, ecosystem processes are shaped by complex interactions between biotic and abiotic components, complicating their predictability. We evaluated how close we can get to ecosystem-level decomposition (*i.e. in situ* litter mixtures decomposition) based on aggregated functional traits (calculated as weighted averages of species litter quality and decomposability) in mountain grasslands patches of central Argentina. We found that aggregated functional traits were not significantly correlated to *in situ* decomposition; *i.e.* contrary to other works, in our system it is not possible to scale up from species characteristics to ecosystem-level decomposition. This pattern was consistent when litter quality and decomposability were weighted by either species standing biomass or by litter input. These two ways of aggregation were highly correlated, indicating that standing biomass was a good proxy of the contribution that species make to litter layer. Aggregated functional traits were strongly associated to litter mixtures decomposability (a proxy for community-level decomposition), indicating that there are no strong interactions among litters of the species decomposing together. However, litter mixtures decomposability was not correlated to *in situ* decomposition, showing that community-level and ecosystem-level decomposition were not related. We suggest that the soil environment generated by vegetation structure of the different grassland patches could be controlling *in situ* decomposition. The prediction of decomposition and nutrient cycling changes associated to land-use change calls for the consideration of variables which integrate different controls; *i.e.* not only species identity and abundance, but also climate and microclimate. In particular, studies combining decomposability and *in situ* decomposition could help to more accurately understand and predict the different mechanisms involved in nutrient and carbon cycling.

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1. Introduction

During the last decades considerable research effort has been directed to understand species effects on ecosystem processes (Wardle et al., 1998; Díaz et al., 2013). In this quest, plant functional traits (*i.e.* vegetative or reproductive characteristics which

influence plant response to environment and/or plant effects on ecosystem functioning, Pérez-Harguindeguy et al., 2013) have been indicated as a simple tool to predict changes in ecosystem processes from shifts in plant communities (Lavorel and Garnier, 2002; Tardif et al., 2014). The rationale behind this approach is that, in addition to their direct effects, environmental factors (*e.g.* climate) and disturbance-related factors (*e.g.* herbivory pressure) affect ecosystem functioning indirectly through their influence on plant species' abundance. Plant species, in turn, affect ecosystem processes through their functional traits (Díaz, 2001; Lavorel and Garnier, 2002). As dominant species concentrate a large proportion of the biomass of a given community, energy and nutrient fluxes and, therefore, ecosystem functioning would depend mostly

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on their trait values (the ‘mass ratio hypothesis’ proposed by Grime, 1998). Based on the previous view, to predict ecosystem functioning based on species functional traits, the values of those traits have to be weighted by the abundance of the species. These weighted traits are defined as ‘aggregated functional traits’, also known as community weighted means (Fig. 1, Díaz and Cabido, 1997; Lavorel and Garnier, 2002). This scaling-up approach from species to ecosystems has been tested on different properties such as primary productivity (e.g. Vile et al., 2006), temporal stability of the communities (e.g. Polley et al., 2007), biomass pools and fluxes, water use and light interception (Mokany et al., 2008), and litter decomposition (e.g. Garnier et al., 2004).

Decomposition is a fundamental process in the regulation of organic matter pools, nutrient cycling and energy fluxes (Chapin et al., 2002). In the context of actual and predicted global changes and their consequences for human well being, there is an urgent need to understand decomposition and its potential feedback on climate and on carbon stocks (IPCC, 2007). Decomposition is regulated by three main factors: environmental conditions, litter quality and the community of decomposers (Swift et al., 1979). Litter quality, e.g. N and lignin content, determines the potential of species litter to decompose (hereafter “single species litter decomposability”, Figs. 1 and 2a, Cornelissen, 1996; Cornwell et al., 2008; Pérez-Harguindeguy et al., 2013). At a local scale, when environmental conditions remain relatively constant, litter quality may play a determinant role for decomposition rates (Lavelle et al., 1993; Aerts, 1997; Cornwell et al., 2008). Several studies have shown that litter quality-related traits weighted by species’ standing biomass (hereafter “biomass-aggregated” litter quality) can be reliable predictors of the natural litter mixtures decomposability, which has been considered as an indicator of decomposition at the community level (Figs. 1 and 2b, Garnier et al., 2004, 2007; Cortez et al., 2007; Quedsted et al., 2007; Fortunel et al., 2009; Pakeman et al., 2010; Furey et al., 2014). However, scaling-up from the species to ecosystem level should aim at predicting actual decomposition as it occurs in the field, under the influence of both biotic and abiotic factors (Garnier et al., 2007; Tardif et al., 2014).

Up to now, only Garnier et al. (2004), Cortez et al. (2007) and Quedsted et al. (2007) specifically tested the feasibility of scaling-up decomposition from species to ecosystems. They studied gradients of vegetation patches at different successional stages and thus, with

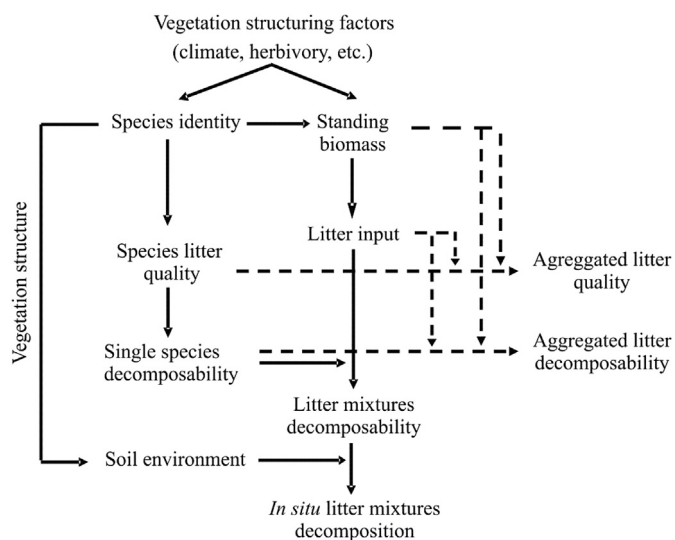


Fig. 1. Scaling-up approach to predict actual decomposition from species to ecosystem level. Dotted arrows relate variables used for calculating aggregated functional traits (litter quality and decomposability) in both ways (standing biomass and litter input).

different plant composition. All these works analyzed the relationship between aggregated functional traits related to litter quality (leaf dry matter content, specific leaf area, etc.) and *in situ* litter mixtures decomposition (i.e. decomposition of natural litter mixtures incubated in the same site where the litter was collected, Figs. 1 and 2c), which is the closest estimate of actual decomposition as it occurs naturally in the ecosystem (Quedsted et al., 2005). From these tests, only Garnier et al. (2004) and Cortez et al. (2007) found that biomass-aggregated litter quality traits were associated to *in situ* decomposition along vegetation gradients. Despite the success reported with these two studies, it is not new that ecosystem processes are shaped by complex interactions between component species and between species and abiotic conditions, and thus, they may be not always easy to predict (Swift et al., 1979; Tardif et al., 2014). Regarding decomposition, we can easily imagine on at least three factors that may interfere with our ability to scale up from species to ecosystem level.

First, if litter input is not directly related with standing biomass, species standing biomass may not be driving decomposition at the community or ecosystem level. In fact, some authors have shown that litter input can differ from that expected from standing biomass depending on species’ leaf longevity (Aerts, 1995) and on particular *in situ* conditions (Barlow et al., 2007; Hansen et al., 2009). In line with this, Quedsted et al. (2007) found that the correlation between aggregated functional traits (leaf dry matter content, specific leaf area, and leaf nitrogen and carbon content) and *in situ* litter mixtures decomposition was significant only when the functional traits were weighted by growth forms contribution to the litter layer (“litter input-aggregated” functional traits hereafter), but not when weighted by species standing biomass, as it is most frequently done.

Second, litters decomposing in mixtures may interact chemically, physically or through microorganisms’ activities. Those interactions may determine a lower or higher decomposability than the one expected by the weighted average of its components (Hättenschwiler et al., 2005; Pérez-Harguindeguy et al., 2008; Cuchietti et al., 2014). Although this increase or decrease in decomposition due to litter mixtures interactions can be low, some experiments show that it can be as much as 20–30% or even 65% in extreme cases (Gartner and Cardon, 2004).

Third, soil environment (soil physicochemical and biological properties, as well as microclimate) can also affect decomposition at local scales (Hector et al., 2000; Orwin et al., 2006). Specifically, vegetation structure, soil type, and the community of microorganisms may significantly affect soil environmental conditions for decomposition changing the actual decomposition patterns from that expected by the weighted average of the component species (Swift et al., 1979; Eviner and Chapin, 2003; Bardgett, 2005).

In this context, we aimed to test if we can scale up decomposition from species to ecosystem level in mountain grasslands of central Argentina (Fig. 1). Based on the mass ratio hypothesis, we compared *in situ* litter mixtures decomposition with aggregated functional traits (litter quality traits and decomposability itself). In addition, we specifically assessed the effect of three possible factors which may challenge our capability to scale up decomposition from species to ecosystem level: (a) litter input (compared to standing biomass), (b) litter interactions during decomposition in litter mixtures, and (c) the soil environment where litter is decomposing.

2. Materials and methods

2.1. Study area

The study was conducted in Pampa de Achala, a high plateau located at the upper belt of Córdoba mountains in central Argentina

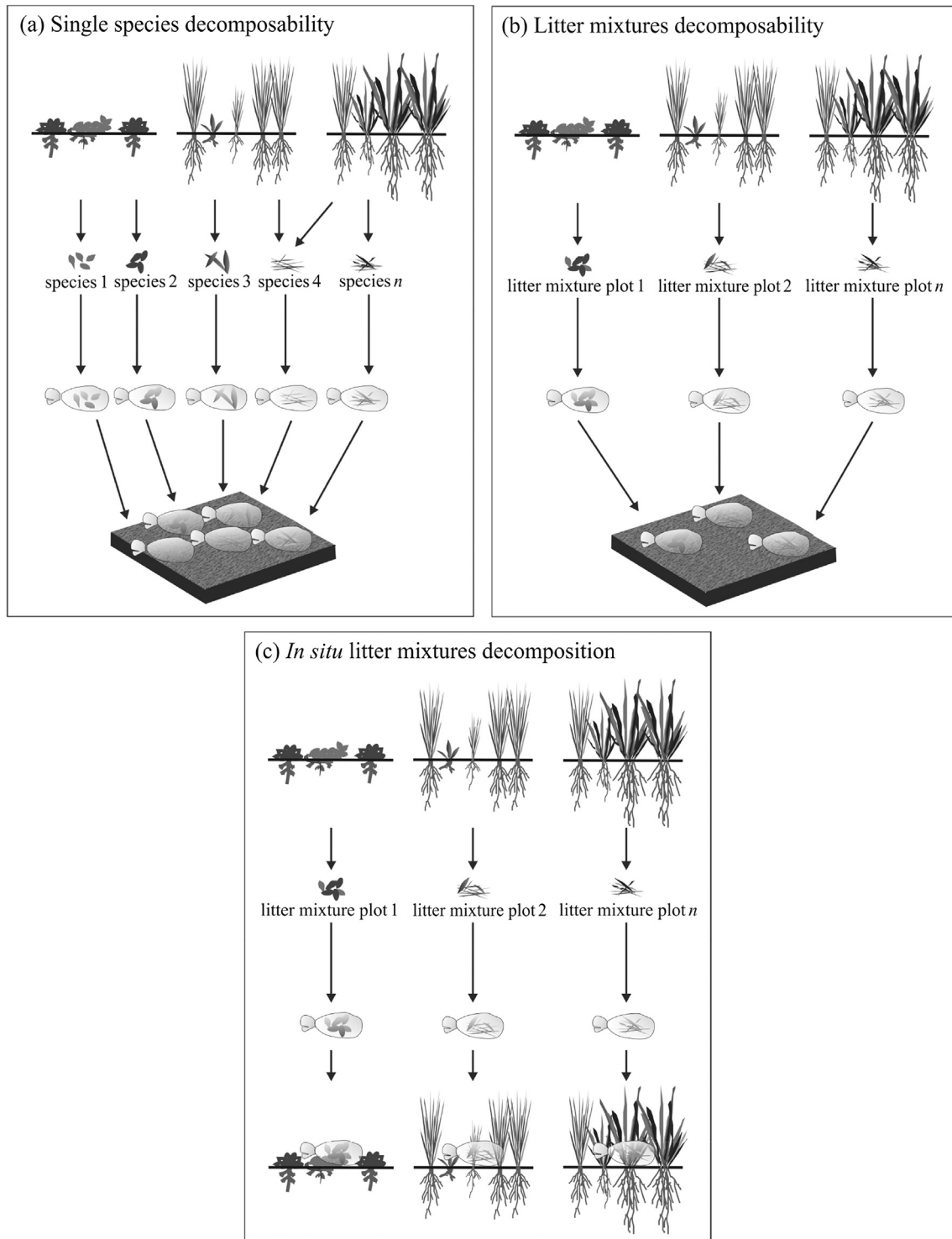


Fig. 2. (a) Single species decomposability: simultaneous incubation of single species in a common garden. (b) Litter mixtures decomposability: simultaneous incubation of litter mixtures from different plots in a common garden. The dry weight loss (%) in (a) and (b) is the result of the structural and chemical properties of the substrates, and thus constitutes an expression of its quality for microorganisms in relation to other substrates within the same common garden. In particular, the dry weight loss (%) in (b) also accounts for the possible interactions between the litters within the mixtures. (c) *In situ* litter mixtures decomposition: incubation of litter mixtures in the same plots where the litter mixtures were collected. The dry weight loss (%) in (c) is the joint result of the substrate quality and litter interaction in combination with the soil environment where the substrates are incubated, *i.e.* soil physicochemical and biological properties, as well as microclimate.

(31° 34' S, 64° 50' W) at 2100 m a.s.l. Mean annual temperature is 8 °C with no frost-free period. Mean annual precipitation is 900 mm, with most rainfall concentrated in the warmest months, between October and April (Cabido and Acosta, 1985; Colladon

et al., 2010). The landscape is a mosaic of grasslands, granitic outcrops and *Polylepis australis* Bitter woodlands (Cabido and Acosta, 1985; Cingolani et al., 2004). The main economic activity is livestock raising, mainly cattle and sheep, which started at the

beginning of the 17th century and completely replaced large native herbivores by the beginning of the 20th century (Díaz et al., 1994). The study was performed in Quebrada del Condorito National Park, where domestic livestock are maintained in some areas to preserve vegetation patchiness and hence plant biodiversity (Cingolani et al., 2010). When grazed by large herbivores, the landscape presents a mosaic of lawn patches and closed and open tussocks grasslands with species of different foliar quality (Cingolani et al., 2003, 2014; Vaieretti et al., 2013). Lawns, where herbivores tend to congregate, are dominated by short palatable plant species such as forbs and graminoids, with high nutrient content and foliar attributes suggesting high relative growth rates. Closed tussock grasslands are dominated by tall tussock grasses and are less used by the herbivores. Open tussock grasslands have a mixture of short vegetation and tussock species (Pucheta et al., 1998; Cingolani et al., 2007; Vaieretti et al., 2010, 2013).

In this study, we used a paddock with low to moderate cattle grazing (0.15–0.20 Cattle Equivalents per ha of vegetated land, *i.e.* discounting rock surface). We selected a representative area of about 225 ha within the paddock. In this area we chose 10 different sites (about 15 m × 15 m) for each of the three vegetation patch types (lawn, open tussock grassland and closed tussock grassland, N = 30). All sites were located at similar altitudes (2150–2200 m a.s.l.) and on gentle slopes (1–5%) distributed across the dominant topographic positions present in the area. Soil organic carbon (C) content is 2.5–9.0 %, the total N content is 0.2–0.7 % and pH is 4.5–5.4 (for further details related to soil physicochemical properties see Vaieretti et al., 2010, 2013).

2.2. Species selection

In February 2006 we made floristic surveys at each of the 30 sites within a 4 m × 4 m plot, and we registered the complete floristic composition. We visually estimated species cover in 5% categories (10%, 15%, 20%, etc.) except for low cover values (<10%), which were estimated in 1% categories (1%, 2%, etc.). When cover was far less than 1%, we registered 0.1% for species present. From these data we calculated the relative cover of each species. Then we selected only the most abundant species, until 80% cover was reached in each floristic sample (following Garnier et al., 2004; Pakeman and Quested, 2007; Pérez-Harguindeguy et al., 2013). By this method we selected a total of 21 species (Appendix A, Table A1) for further measurements and analyses. Species' nomenclature follows Zuloaga et al. (2008) and its online actualization (www.darwin.edu.ar).

2.3. Plant volume as a surrogate of biomass

Several studies use surrogates of standing biomass such as cover, frequency, allometric equations and others, instead of measuring biomass itself (*e.g.* Quested et al., 2007; Garnier et al., 2007). Previous findings in our study area (Pucheta et al., 2004) indicated that the volume of the vegetation (estimated through the average height and the cover proportion in a given area) was strongly related to its actual biomass. Thus, we measured the height of the vegetative fraction of six representative adult plants of each of the 21 selected species. These measures were not associated to the plots, but measured across the sites since individual height of most species is similar across patches. The average height (cm) of the different species multiplied by their cover (cm², calculated from the percent cover in the 4 m × 4 m plot) was the volume estimation (cm³) of each species at each plot. Only when species were very variable in height according to the patch type, we measured heights in each patch type and used the average height of the species for each particular patch type for the estimations.

2.4. Litter input estimation

We used data from Vaieretti et al. (2013) to estimate litter input of the study sites. Four to six permanent squares (1 m × 1 m) were randomly distributed within each site to estimate the annual litter input rate (g m⁻²). Each square was cleared of all litter at the beginning of autumn (April 2006) and accumulated litter from each square (sub-samples) was collected in August 2006, October 2006 and May 2007. At the laboratory, litter was dried at 60 °C, until constant weight was attained. Then, the proportion of each growth form in the litter sub-samples was visually estimated. Proportion of species could not be estimated since many of the species were not recognizable from senesced tissues. The growth forms considered were: tussock grasses with thick leaves (mainly *Poa stuckertii* (Hack.) Parodi, hereafter “thick tussock grasses”), tussock grasses with thin leaves (mainly *Deyeuxia hieronymi* (Hack.) Turpe and *Festuca lilloi* Hack., hereafter “thin tussock grasses”), *Eryngium agavifolium* Griseb., perennial graminoids, annual graminoids (mainly *Muhlenbergia peruviana* P. Beauv. Steud.) and forbs (Vaieretti et al., 2013). The difference between tussocks and graminoids is principally size; the first are much taller and erect than the second ones. In addition, tussocks are perennial while graminoids can be perennial or annual (Díaz and Cabido, 1997). *E. agavifolium* was considered as a separate group because its rosettes are very different from the rest of the rosettes (Díaz and Cabido, 1997; Díaz et al., 1998). The dry weight of each growth form sub-sample was calculated for each date by multiplying the growth form proportion in the litter layer by the total dry weight of the sub-sample. The values of all sub-samples were averaged to obtain one value per growth form per site. Finally, the annual litter input of each growth form was calculated by summing up the values of all dates, and the total annual litter input by summing up the values of all growth forms (of the 21 species described above). For further details see Vaieretti et al. (2013). The procedure is similar to that used by Quested et al. (2007).

2.5. Single species decomposability (Fig. 2a)

Data on single species decomposability was obtained from Poca et al. (2014). To determine decomposability (percentage of dry weight loss) of the 21 selected dominant species litter was randomly collected across all sites. 20 litterbags for each of the 21 species of 0.3 mm mesh nylon were made and filled with 1 g of air-dried material, following Cornelissen (1996) and Pérez-Harguindeguy et al. (2013).

In an ungrazed paddock within the study area a decomposition bed was prepared where all litterbags were simultaneously incubated; *i.e.* decomposability is a relative term to the substrates incubated together in a common garden (further details in Fig. 2a). Litter bags were placed randomly on the soil surface, where vegetation and litter were previously removed, with one side in contact with the ground. Then all the litter bags were covered with a fine layer of litter from the area to simulate natural conditions of decomposition. Litterbags were incubated for either 10 or 28 weeks (from December 2008 to March 2009 and from December 2008 to July 2009 respectively). At each date 10 litterbags for each species were retrieved. After incubation, all samples were stored at –14 °C until processing. Once defrosted, adhering soil, soil fauna and other extraneous materials were removed. Samples were oven-dried for at least 48 h at 60 °C, and then weighed. Initial dry mass was calculated from the water content of a subsample that was weighed simultaneously to the samples when the litterbags were built, oven-dried until constant weight at 60 °C and then re-weighed. Decomposability of each sample was estimated as the percentage of dry weight loss at the end of the incubation period (Cornelissen, 1996). Samples were averaged to obtain one value per species per

incubation period. As litter dry weight loss after the two incubation periods was highly correlated ($r = 0.91$, $P \leq 0.001$), for all the calculations and relationships here explored, we only used the dry weight loss of the first incubation period as an estimator of decomposability. Consistently, in previous studies, this period (ten weeks) seemed adequate to capture the decomposition dynamic in the study area (Vaieretti et al., 2010, 2013).

2.6. Single species litter quality

Data of single species litter quality was obtained from Poca et al. (2014). As parameters of litter quality we selected: nitrogen, lignin, cellulose and hemicellulose content. Nitrogen content was determined using an Autoanalyser (RFA 300-Alpken, Wilsonville, O.R., USA) following O'Neill and Webb (1970). Lignin, cellulose and hemicellulose content were determined following the technique of Goering and Van Soest (1970). We considered the sum of these three variables ("fiber content" hereafter), as an additional indicator of litter quality since it is a functional trait that integrates all the recalcitrant components of the litter. At species level fiber content was one of the litter quality traits that better correlated to litter decomposability (Poca et al., 2014).

2.7. Aggregated functional traits (Fig. 1)

To scale from species to ecosystems we calculated aggregated functional traits (nitrogen and fiber content and litter decomposability itself) as follows:

Biomass-aggregated. This weighted average was estimated for each site as the volume-weighted average of the 21 selected dominant species:

$$\text{Biomass – aggregated traits} = \sum_{i=1}^n p_i \text{ trait}_i$$

Where p_i is the relative volume of each species (indicator of its relative biomass) within each site, n is 21 (the number of selected species) and trait_i is the value of the trait (litter decomposability, nitrogen or fiber content) for the species i . The relative volume was calculated considering only the 21 species under study.

Litter input-aggregated. This average was calculated based on the input of litter of the different growth forms as follows:

$$\text{Litter input – aggregated traits} = \sum_{j=1}^n l_j \text{ trait}_j$$

Where l_j is the relative litter production of the growth form j within each site, n is the number of growth forms at each site, trait_j is the value of the trait (litter decomposability, nitrogen or fiber content) for the growth form j . When the growth form had more than one species, this value was calculated as an average of the values of the component species of that growth form. In a previous study in the area it has been demonstrated that these traits were more variable between than within growth forms (Poca et al., 2014).

2.8. Litter mixtures decomposability, in situ decomposition and quality (Figs. 1, 2b and 2c)

We used data of *in situ* litter mixtures decomposition, litter mixtures decomposability (as indicators of ecosystem- and

community-level decomposition respectively) and quality from Vaieretti et al. (2013). To obtain these data, in September 2006, Vaieretti et al. (2013) collected a sample of naturally shed mixed litter from the soil surface in each site. The authors measured litter mixtures' decomposability by incubating litter mixtures in a common garden experiment following the same procedure as the one described in Section 2.5 for the 21 single species. In addition, they obtained *in situ* litter mixtures decomposition through the incubation of litter mixtures in the same sites where the mixtures were collected. Vaieretti et al. (2013) used for both experiments the same litterbag methodology as the one explained in Section 2.5 for the species common garden experiment. They measured litter mixtures quality (nitrogen and fiber content) through the same methods used to determine single species litter quality. They measured the quality parameters in the mixture, representing in this way the average quality of the component species altogether. For further details see Vaieretti et al. (2013).

2.9. Data analysis

To evaluate the association between the variables measured we used Pearson correlations, where the sampling unit was the plot ($N = 30$). In Fig. S1 of the Supplementary Material we show the scheme of the data analysis that is described in this section. This same scheme is used later for showing the results (see Fig. 3). Only to corroborate that litter quality traits were associated with decomposability, we tested if biomass-aggregated nitrogen and fiber content were related with biomass-aggregated decomposability (Fig. S1 arrow A), and that litter mixtures quality (litter mixtures nitrogen and fiber content) were related with litter mixtures decomposability (Fig. S1 arrow M).

We tested how well we can scale up from single species functional traits to ecosystem-level decomposition by correlating biomass-aggregated traits (nitrogen, fiber content and decomposability) to *in situ* litter mixtures decomposition (Fig. S1 arrows B and C).

We correlated biomass-aggregated decomposability with litter input-aggregated decomposability, and the same was done for both litter quality traits (nitrogen and fiber content) to analyze if standing biomass is representative of the litter input as a weighting factor. Furthermore, we tested if we can scale up from species to ecosystem-level by correlating the litter input-aggregated quality

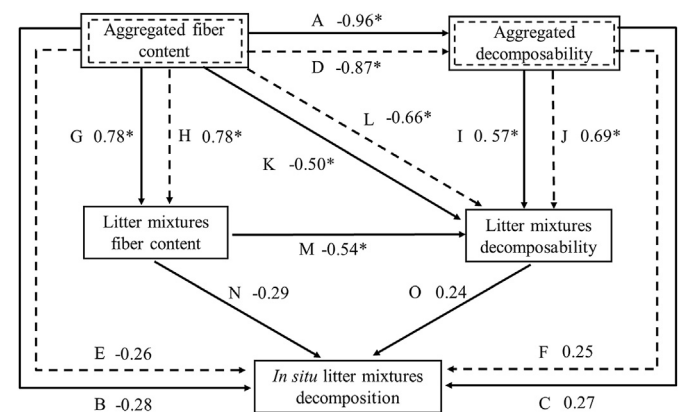


Fig. 3. Correlations among aggregated fiber content and decomposability and community and ecosystem-level decomposition. Capital letters indicate the reference of the relationships, while numbers correspond to correlation coefficients. Full arrows indicate correlations with biomass-aggregated traits while dotted arrows indicate correlations with litter input-aggregated traits. Significant correlations ($P \leq 0.01$) are shown with an asterisk (*), while marginally significant correlations ($0.01 < P \leq 0.1$) are indicated with the initials "ms".

and/or decomposability to *in situ* litter mixtures decomposition (Fig. S1 arrows E and F), instead of biomass-aggregated litter quality and/or decomposability (Fig. S1 arrows B and C). Then, all possible correlations with biomass-aggregated quality and/or decomposability on the one hand (Fig. S1 arrows A, G, K and I), and with litter input-aggregated litter quality and/or decomposability on the other hand (Fig. S1 arrows D, H, L, and J), were performed. A similar degree of association would indicate that standing biomass of each species in the community is indeed reflected in the contribution that the species makes to the litter layer. However, if litter-aggregated trait values are more strongly associated than biomass-aggregated ones it would indicate that the standing biomass of the species is a poor indicator of their contribution to the litter layer.

We correlated biomass-aggregated and litter input-aggregated decomposability with litter mixtures decomposability to evaluate a possible effect of litter interactions between the component species of litter mixtures (Fig. S1 arrows I and J). Strong associations between those variables would imply that non-additive interactions between species in mixtures would not be big enough to challenge predictions based on weighted averages; and that we can easily scale up from species to community-level decomposition. Furthermore, we explored an additional way to evaluate a possible effect of litter interactions between the component species of litter mixtures performing a correlation between biomass-aggregated litter quality traits (nitrogen and fiber content) and litter mixtures decomposability (Fig. S1 arrow K and L).

Finally, we correlated litter mixtures quality and decomposability with *in situ* litter mixtures decomposition (Fig. S1 arrows N and O respectively). We considered that strong correlations would indicate a strong influence of those variables in actual decomposition (*i.e.* ecosystem level-decomposition) showing that the micro-environmental conditions do not modify substantially the patterns expected by litter mixtures traits.

We tested homoscedasticity and normality of residuals with Levene and Kolmogorov–Smirnov tests, respectively. We used a $P \leq 0.01$ of significance. We did not perform a Bonferroni correction to avoid the increase of type II error (Cabin and Mitchell, 2000), but we lowered the P-value of significance to avoid the increase of type I error. We did not attempt to perform a structural equation modeling because we were not interested in partial correlation coefficients since the main relationships were not significant (see Fig. 3 arrows B, E and C and F). On regards to the heterogeneity of the data coming from different years (with probably different temperatures, humidity, etc.) we consider it is not relevant since we are not comparing *in situ* experiments of different years, but different common gardens and common gardens with *in situ* incubations. For all the statistical analyses reported above we used the package SPSS Inc (version 17.0).

3. Results

As results obtained through the analysis for nitrogen and for fiber content followed the same trends (though the signs of correlations were opposite) we only described the results obtained for aggregated fiber content as an example (Fig. 3). The results obtained for aggregated nitrogen content are shown in the Appendix (Appendix A1, Fig. A1).

As expected, biomass-aggregated fiber content and biomass-aggregated decomposability were strongly correlated (Fig. 3 arrow A). Also, litter mixtures fiber content was significantly correlated to its decomposability (Fig. 3 arrow M). However, *in situ* litter mixtures decomposition was not significantly correlated with biomass-aggregated fiber content (Fig. 3 arrow B) or with biomass-aggregated decomposability (Fig. 3 arrow C and Fig. 4a). In other

words, *in situ* litter mixtures decomposition was not explained by the dominant species' traits (litter quality and decomposability) and abundance.

Biomass-aggregated traits were strongly correlated with litter input-aggregated traits ($r = 0.90$, $P \leq 0.001$ for fiber content; and $r = 0.94$, $P \leq 0.001$ for decomposability). However, as with biomass-aggregated traits, *in situ* litter mixtures decomposition was neither correlated with litter input-aggregated fiber content nor with decomposability (Fig. 3 arrows E and F). In addition, all the remaining relationships here explored through both ways of aggregation of the traits were qualitatively similar in significance and degree of association (Fig. 3 arrows A, G, K and I compared to D, H, L, and J). These results suggest that species standing biomass is a good estimator of the contribution that species make to the litter layer at each site, for the physiognomies present in the studied grasslands.

We found that both biomass-aggregated and litter input-aggregated decomposability were significantly correlated with litter mixtures decomposability (Fig. 3 arrow I and Fig. 4b and Fig. 3 arrow J, respectively). This indicates that there are no strong interactions between litters of the species decomposing together in the litter mixtures. This idea was reinforced by the significant correlation between biomass and litter input-aggregated fiber content and litter mixtures decomposability (Fig. 3 arrow K and L).

In situ litter mixtures decomposition was not significantly correlated with litter mixtures fiber content or decomposability (Fig. 3 arrows N and O respectively). That is, ecosystem-level decomposition was not associated with community-level quality or decomposition.

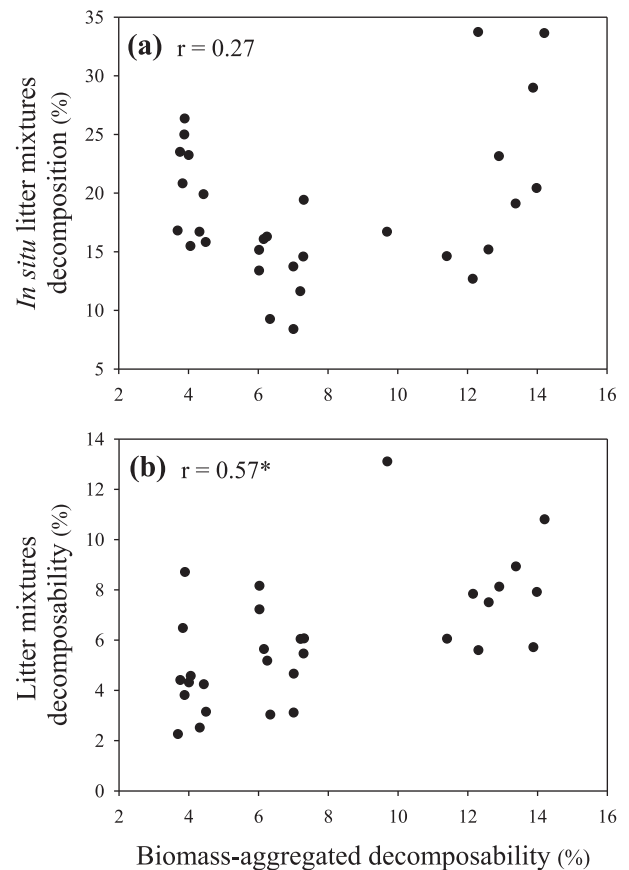


Fig. 4. Scatter plots of biomass-aggregated decomposability (% of dry weight loss) against (a) *in situ* litter mixtures decomposition (% of dry weight loss) and (b) litter mixtures decomposability (% of dry weight loss). Correlation coefficients are indicated in the plots. Significant relationships ($P \leq 0.01$) are shown with an asterisk (*).

4. Discussion

Our results show that we cannot scale up decomposition from species to ecosystem level as easily as we can scale up from species to communities for the grassland patches in central Argentina here under study. This means that using aggregated functional traits of the dominant species we can successfully predict community-level decomposition (*i.e.* litter mixtures decomposability, encompassing litter quality and the interactions between the litters within the mixtures) but not ecosystem-level decomposition (*i.e.* *in situ* litter mixture decomposition, comprising not only litter quality and interactions but also the soil environment where the litter mixtures were incubated). In this sense, the only difference between litter mixtures decomposability and *in situ* decomposition is the environment where they were incubated. Therefore, the soil environmental conditions seem to be the cause by which ecosystem-level decomposition cannot be scaled up from dominant species' litter quality and decomposability.

We found that biomass estimations can be a good proxy of litter input. In this sense, our results disagree with [Quested et al. \(2007\)](#) who found that aggregated functional traits calculated on the basis of litter input related better to *in situ* litter mixtures decomposition than those on the basis of biomass. It is important to distinguish that [Quested et al. \(2007\)](#) found that 90% of the standing biomass corresponded to woody species but the litter layer did not show the same composition. The communities under study here have scarce woody species and most of the species are forbs, graminoids and tussocks (generally with shorter leaf lifespan than woody species). This is probably the reason why the relationship between standing biomass and litter is tighter in our study. In other words, the similarity between standing biomass and litter input composition could depend on the vegetation structure and the leaf lifespans of the system under study.

We also found a tight correlation between aggregated functional traits and litter mixture decomposability; that is to say that litter interactions in mixtures do not hinder the scaling-up from species to communities. This does not mean that litter of different species do not interact within mixtures, but that the magnitude of that interaction, if occurring, is not strong enough to affect the general patterns of decomposability. Our results are in line with previous works where the magnitude of variation in decomposition due to the interaction of species in a litter mixture is very low, although sometimes significant, in comparison to differences due to their average quality ([Pérez-Harguindeguy et al., 2008](#); [Hoorens et al. 2010a,b](#); [Cuchietti et al., 2014](#); but see: [Gartner and Cardon, 2004](#)).

Although dominant species do control community-level decomposition through their litter quality and decomposability; they do not seem to control ecosystem-level decomposition in the grassland patches analyzed. Our results show that lawns, dominated by species with higher litter quality (lower fiber content and higher nitrogen content), do have higher decomposability. But, the higher decomposability does not necessarily lead to faster *in situ* litter mixtures decomposition, compared to tussocks dominated by species of lower litter quality and decomposability. Therefore, our results are somehow in disagreement with general models of decomposition which predict that at the local scale litter quality always becomes the most important control of litter decomposition ([Lavelle et al., 1993](#); [Aerts, 1997](#)). This is not because litter mixtures quality is not relevant itself as a control, but maybe its variability between patch types is rather small (*e.g.* about 0.3% in N content in comparison to 2% in a similar ecosystem in [Güsewell et al., 2005](#)) compared to the variation of other factors at ecosystem level ([Vaieretti et al., 2013](#)). Complementary to this, [Manning et al. \(2008\)](#) stated that even if at species level there are differences in litter quality and decomposability, these differences will only affect

ecosystem-level decomposition if its magnitude is big enough to override other factors, as it seems to be here the soil environment.

The relevance of soil environment in decomposition patterns has already been shown in studies with standard or common materials (*i.e.* common materials to all the incubation sites and of known quality; as in [Hector et al., 2000](#); [Orwin et al., 2006](#); [Vaieretti et al., 2010](#)). Our results do agree with a previous work ([Vaieretti et al., 2013](#)) in the same study area where the authors found that *in situ* litter mixture decomposition was correlated to common substrates decomposition (litter of two plant species incubated in the different vegetation patch types) but not to litter mixtures quality. The authors suggested that changes in vegetation structure produced by herbivores (*e.g.* in species abundance and identity and consequently in litter quantity accumulated), would be the ultimate driver of microclimatic differences between lawns and tussock grasslands. These differences in microclimate conditions (*e.g.* maximum and minimum soil temperature, and its daily or seasonal variation, as well as variation in soil moisture) may influence microbial abundance and/or its metabolic rates ([Swift et al., 1979](#); [Chapin et al., 2002](#)). In consequence, our work evidences the need of digging deeper into the effect of the soil environment on decomposition (soil physicochemical and biological properties and microclimate) when scaling-up from species to ecosystem level decomposition.

5. Conclusions

Many studies have used the mass ratio conceptual framework in the context of decomposition as a tool to scale up from species traits and abundance to ecosystem processes (see [Garnier et al., 2004, 2007](#); [Cortez et al., 2007](#); [Quested et al., 2007](#); [Fortunel et al., 2009](#); [Pakeman et al., 2010](#); [Furey et al., 2014](#)). Still, only some of these works have incorporated the use of ecosystem-level decomposition ([Garnier et al., 2004](#); [Cortez et al., 2007](#); [Quested et al., 2007](#)). *In situ* litter mixtures decomposition can reflect not only litter quality and litter interactions, as decomposability does, but also the effect of soil environment. Then, this parameter constitutes a more integral surrogate of decomposition as it actually occurs in nature. We highlight the need of more experimental studies where soil environmental variables are accounted. Specifically, through the simultaneous incubation of standard materials and *in situ* litter mixtures, the measurement of soil environmental variables (*e.g.* soil and air temperature and moisture, solar radiation and micro-organisms identity and activity) and manipulation experiments. In the context of global change and its components, the accurate prediction of changes in decomposition and nutrient cycling requires of the measure of parameters which integrate different controls (species identity and abundance, climate and microclimate, etc.). Studies combining decomposability, decomposition of standard materials, *in situ* decomposition and soil environmental variables could help to better understand and predict the different mechanisms involved in ecosystem functioning, particularly the rates of nutrient cycles, and their potential feedback on climate and carbon stocks.

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Appendix A

Table A1

Scientific name, family and growth form of the 21 dominant species of the 30 sites under study that represent the 80% of cover in each floristic sample.

Species	Family	Growth form
<i>Bidens andicola</i> var. <i>decomposita</i> Kunth	Asteraceae	Forb
<i>Bromus catharticus</i> var. <i>catharticus</i> Vahl	Poaceae	Graminoid
<i>Carex fuscula</i> ssp. <i>fuscula</i> d'Urv.	Cyperaceae	Graminoid
<i>Chascolytrum subaristatum</i> (Lam.) Desv.	Poaceae	Graminoid
<i>Deyeuxia hieronymi</i> (Hack.) Türpe	Poaceae	Tussock grass
<i>Eleocharis pseudoalbibracteata</i> S. González & Guagl.	Cyperaceae	Graminoid
<i>Eragrostis lugens</i> Nees.	Poaceae	Graminoid
<i>Eryngium agavifolium</i> Griseb.	Apiaceae	<i>Eryngium agavifolium</i>
<i>Eryngium nudicaule</i> Lam.	Apiaceae	Forb
<i>Festuca dissitiflora</i> Steud. ex Griseb.	Poaceae	Graminoid
<i>Festuca lilloi</i> Hack.	Poaceae	Tussock grass
<i>Grindelia globularifolia</i> Griseb.	Asteraceae	Forb
<i>Juncus pallescens</i> var. <i>achalensis</i> Lam.	Juncaceae	Graminoid
<i>Juncus uruguensis</i> Griseb.	Juncaceae	Graminoid
<i>Lachemilla pinnata</i> (Ruiz & Pav.) Rothm.	Rosaceae	Forb
<i>Muhlenbergia peruviana</i> (P. Beauv.) Steud.	Poaceae	Graminoid
<i>Nassella nidulans</i> (Mez) Barkworth	Poaceae	Tussock grass
<i>Plantago argentina</i> Pilg.	Plantaginaceae	Forb
<i>Poa hubbardiana</i> Parodi	Poaceae	Graminoid
<i>Poa stuckertii</i> (Hack.) Parodi	Poaceae	Tussock grass
<i>Sisyrinchium unguiculatum</i> Griseb.	Iridaceae	Graminoid

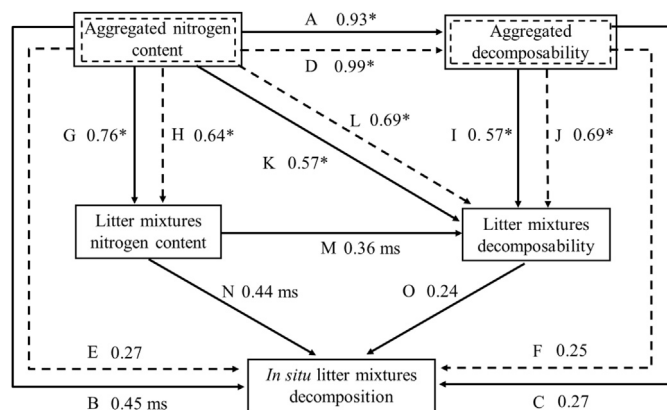


Fig. A1. Correlations among aggregated nitrogen content and decomposability and community and ecosystem-level decomposition. Capital letters indicate the reference of the relationships, while numbers correspond to correlation coefficients. Full arrows indicate correlations with biomass-aggregated traits while dotted arrows indicate correlations with litter input-aggregated traits. Significant correlations ($P \leq 0.01$) are shown with an asterisk (*), while marginally significant correlations ($0.01 < P \leq 0.1$) are indicated with the initials "ms".

Appendix B. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2015.02.005>.

References

- Aerts, R., 1995. The advantages of being evergreen. *Trends Ecol. Evol.* 10, 402–407.
- Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79, 439–449.
- Bardgett, R.D., 2005. The soil environment. In: Crawley, M.J., Little, C., Southwood, T.R.E., Ulfstrand, S. (Eds.), *The Biology of Soil: a Community and Ecosystem Approach*. Oxford University Press, Oxford, NY, pp. 1–23.
- Barlow, J., Gardner, T.A., Ferreira, L.V., Peres, C.A., 2007. Litter fall and decomposition in primary, secondary and plantation forests in the Brazilian Amazon. *For. Ecol. Manag.* 247, 91–97.
- Cabido, M., Acosta, A., 1985. Estudio fitosociológico en bosques de *Polylepis australis* BITT. ("Tabaquito") en las Sierras de Córdoba, Argentina. *Documm. Phytosociol.* 9, 385–400.
- Cabin, R.J., Mitchell, R.J., 2000. To Bonferroni or not to Bonferroni: when and how are the questions. *Bull. Ecol. Soc. Am.* 81, 246–248.
- Chapin III, F.S., Matson, P.A., Moonley, H.A., 2002. *Principles of Terrestrial Ecosystem Ecology*. Springer-Verlag, New York, New York, USA.
- Cingolani, A.M., Cabido, M., Renison, D., Solís Neffa, V., 2003. Combined effects of environment and grazing on vegetation structure in Argentine granite grasslands. *J. Veg. Sci.* 14, 223–232.
- Cingolani, A.M., Renison, D., Zak, M., Cabido, M., 2004. Mapping vegetation in a heterogeneous mountain using Landsat data: an alternative method to define and classify land-cover units. *Remote Sens. Environ.* 92, 84–97.
- Cingolani, A.M., Cabido, M., Gurrich, D.E., Renison, D., Díaz, S., 2007. Filtering processes in the assembly of plant communities: are species presence and abundance driven by the same traits? *J. Veg. Sci.* 18, 911–920.
- Cingolani, A.M., Vaieretti, M.V., Gurrich, D.E., Giorgis, M.A., Cabido, M., 2010. Predicting alpha, beta and gamma plant diversity from physiognomic and physical indicators as a tool for ecosystem monitoring. *Biol. Conserv.* 143, 2570–2577.
- Cingolani, A.M., Vaieretti, M.V., Giorgis, M.A., Poca, M., Tecco, P.A., Gurrich, D.E., 2014. Can livestock grazing maintain landscape diversity and stability in an ecosystem that evolved with wild herbivores? *Perspect. Plant Ecol. Evol. Syst.* 16, 143–153.
- Colladon, L., Felici, G.S., Pazos, I., 2010. Anuario Pluviométrico 2005/6–2009/10. Cuenca del Río San Antonio. Sistema del Río Suquia-Provincia de Córdoba. Instituto Nacional del agua y del ambiente (INA) y centro de investigaciones de la Región Semiárida (CIRSA).
- Cornelissen, J.H.C., 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *J. Ecol.* 84, 573–582.
- Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., et al., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol. Lett.* 11, 1–7.
- Cortez, J., Garnier, E., Pérez-Harguindeguy, N., Debussche, M., Gillon, D., 2007. Plant traits, litter quality and decomposition in a Mediterranean old-field succession. *Plant Soil* 296, 19–34.
- Cuchietti, A., Marcotti, E., Gurrich, D.E., Cingolani, A.M., Pérez Harguindeguy, N., 2014. Leaf litter mixtures and neighbour effects: low-nitrogen and high-lignin species increase decomposition rate of high-nitrogen and low-lignin neighbours. *Appl. Soil Ecol.* 82, 44–51.
- Díaz, S., 2001. Does biodiversity matter to terrestrial ecosystem processes and services? In: Steffen, Will, et al. (Eds.), *Challenges of a Changing Earth: Proceedings of the Global Change Open Science Conference*, Amsterdam, the Netherlands, 10–13 July 2001. Springer.
- Díaz, S., Cabido, M., 1997. Plant functional types and ecosystem function in response to global change: a multiscale approach. *J. Veg. Sci.* 8, 463–474.
- Díaz, S., Acosta, A., Cabido, M., 1994. Community structure in montane grasslands of central Argentina in relation to land use. *J. Veg. Sci.* 5, 483–488.
- Díaz, S., Cabido, M., Casanoves, F., 1998. Functional traits and environmental filters at a regional scale. *J. Veg. Sci.* 9, 113–122.
- Díaz, S., Purvis, A., Cornelissen, J.H., Mace, G.M., Donoghue, M.J., Ewers, R.M., Jordano, P., Pearse, W.D., 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecol. Evol.* 3, 2958–2975.
- Eviner, V.T., Chapin III, F.S., 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annu. Rev. Ecol. Evol. Syst.* 34, 455–485.
- Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., et al., 2009. Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology* 90, 598–611.
- Furey, C., Tecco, P.A., Pérez-Harguindeguy, N., Giorgis, M.A., Grossi, M., 2014. The importance of native and exotic plant identity and dominance on decomposition patterns in mountain woodlands of central Argentina. *Acta Oecol.* 54, 13–20.
- Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., et al., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85, 2630–2637.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., et al., 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Ann. Bot.* 99, 967–985.
- Gartner, T.B., Cardon, Z.G., 2004. Decomposition dynamics in mixed-species leaf litter. *Oikos* 104, 230–246.
- Goering, H.K., Van Soest, P.J., 1970. *Forage Fiber Analyses*. Handbook N° 379. Department of Agriculture, USDA, Washington D.C.

- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910.
- Güsewell, S., Jewell, P.L., Edwards, P.J., 2005. Effects of heterogeneous habitat use by cattle on nutrient availability and litter decomposition in soils an Alpine pasture. *Plant Soil* 268, 135–149.
- Hansen, K., Vesterdal, L., Schmidt, I.K., Gundersen, P., Sevel, L., Bastrup-Birk, A., et al., 2009. Litterfall and nutrient return in five tree species in a common garden experiment. *For. Ecol. Manag.* 257, 2133–2144.
- Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 36, 191–218.
- Hector, A., Beale, A.J., Minns, A., Otway, S.J., Lawton, J.H., 2000. Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. *Oikos* 90, 357–371.
- Hoorens, B., Stroetenga, M., Aerts, R., 2010a. Litter mixture interactions at the level of plant functional types are additive. *Ecosystems* 13, 90–98.
- Hoorens, B., Coomes, D., Aerts, R., 2010b. Neighbour identity hardly affects litter-mixture effects on decomposition rates of New Zealand forest species. *Oecologia* 162, 479–489.
- IPCC, 2007. Climate change 2007: synthesis report. In: Core Writing Team, Pachauri, R.K., Reisinger, A. (Eds.), Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland.
- Lavelle, P., Blanchart, E., Martin, S., Spain, A.V., Toutain, F., Barois, I., Shaefer, R., 1993. A hierarchical model for decomposition in terrestrial ecosystems: applications to soils of the humid tropics. *Biotropica* 25, 130–150.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556.
- Manning, P., Saunders, M., Bardgett, R.D., Bonkowski, M., Bradford, M.A., Ellis, R.J., et al., 2008. Direct and indirect effects of nitrogen deposition on litter decomposition. *Soil Biol. Biochem.* 40, 688–698.
- Mokany, K., Ash, J., Roxburgh, S., 2008. Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *J. Ecol.* 96, 884–893.
- Orwin, K.H., Wardle, D.A., Greenfield, L.G., 2006. Ecological consequences of carbon substrate identity and diversity in a laboratory study. *Ecology* 87, 580–593.
- O'Neill, J., Webb, R., 1970. Simultaneous determination of nitrogen, phosphorus and potassium in plant material by automatic methods. *J. Sci. Food Agric.* 21, 217–219.
- Pakeman, R.J., Quedsted, H., 2007. Sampling plant functional traits: what proportion of the species need to be measured? *Appl. Veg. Sci.* 10, 91–96.
- Pakeman, R.J., Eastwood, A., Scobie, A., 2010. Leaf dry matter content as a predictor of grassland litter decomposition: a test of the 'mass ratio hypothesis'. *Plant Soil* 342, 49–57.
- Pérez-Harguindeguy, N., Blundo, C.M., Gurvich, D.E., Díaz, S., Cuevas, E., 2008. More than the sum of its parts? Assessing litter heterogeneity effect on the decomposition of litter mixtures through leaf chemistry. *Plant Soil* 303, 151–159.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., et al., 2013. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 61, 167–234.
- Poca, M., Pérez-Harguindeguy, N., Vaieretti, M.V., Cingolani, A.M., 2014. Descomposición y calidad físico-química foliar de 24 especies dominantes de los pastizales de altura de las sierras de Córdoba, Argentina. *Ecología Austral* 24, 249–257.
- Polley, H.W., Wilsey, B.J., Derner, J., 2007. Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos* 116, 2044–2052.
- Pucheta, E., Cabido, M., Díaz, S., Funes, G., 1998. Floristic composition, biomass, and aboveground net plant production in grazed and protected sites in a mountain grassland of central Argentina. *Acta Oecol.* 19, 97–105.
- Pucheta, E., Ferrero, E., Heil, L., Schneider, C., 2004. Modelos de regresión para la estimación de la biomasa aérea en un pastizal de montaña de Pampa de Achala (Córdoba, Argentina). *Agriscientia* 21, 23–30.
- Qusted, H., Callaghan, T.V., Cornelissen, J.H.C., Press, M.C., 2005. The impact of hemiparasitic plant litter on decomposition: direct, seasonal and litter mixing effects. *Ecology* 93, 87–98.
- Qusted, H., Eriksson, O., Fortunel, C., Garnier, E., 2007. Plant traits relate whole-community litter quality and decomposition following land use change. *Funct. Ecol.* 21, 1016–1026.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. In: *Studies in Ecology*, vol. 5. Blackwell, Oxford, UK.
- Tardif, A., Shipley, B., Bloor, J.M., Soussana, J.F., 2014. Can the biomass-ratio hypothesis predict mixed-species litter decomposition along a climatic gradient? *Ann. Bot.* <http://dx.doi.org/10.1093/aob/mct304>.
- Vaieretti, M.V., Cingolani, A., Pérez-Harguindeguy, N., Gurvich, D.E., Cabido, M., 2010. Does decomposition of standard materials differ among grassland patches maintained by livestock? *Austral Ecol.* 35, 935–943.
- Vaieretti, M.V., Cingolani, A., Pérez-Harguindeguy, N., Cabido, M., 2013. Effects of differential grazing on decomposition rate and nitrogen availability in a productive mountain grassland. *Plant Soil* 371, 675–691.
- Vile, D., Shipley, B., Garnier, E., 2006. Ecosystem productivity can be predicted from potential relative growth rate and species abundance. *Ecol. Lett.* 9, 1061–1067.
- Wardle, D.A., Barker, G.M., Bonner, K.I., Nicholson, K.S., 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *J. Ecol.* 86, 405–420.
- Zuloaga, F.O., Morrone, O., Belgrano, M.J., 2008. Catálogo de las Plantas Vasculares del Cono Sur (Argentina, Sur de Brasil, Chile, Paraguay y Uruguay). In: *Monogr. Missouri Bot. Garden (USA)*.