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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; Quested 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 Quested 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 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 (Quested 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.

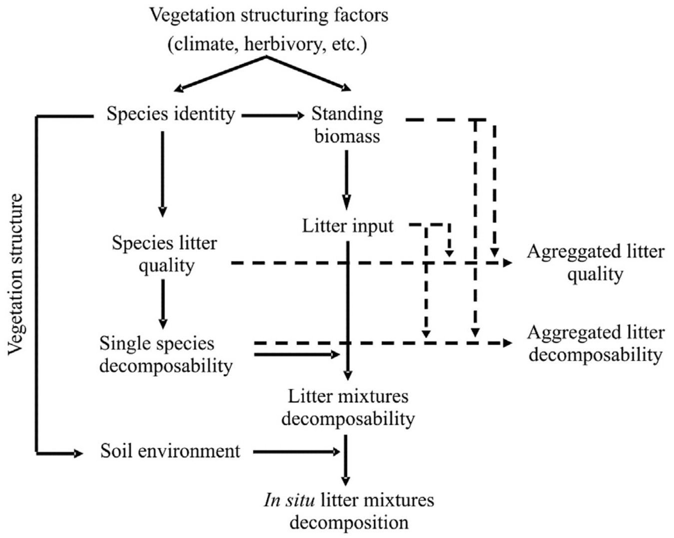

Fig. 1. Scaling-up approach to predict actual decomposition from species to ecosystem level. Dotted arrows relate variables used for calculating aggregated functional traits (litter quality and decomposability) in both ways (standing biomass and litter input).

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, Quested 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

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