

Short communication

Is litter decomposition influenced by forest size and invertebrate detritivores during the dry season in semiarid Chaco Serrano?

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ABSTRACT

Forest loss can affect ecosystem processes such as litter decomposition. In semi-arid areas, where forest loss is increasing, soil fauna can play a particularly important role on litter decomposition. However, few studies have addressed the effect of soil fauna on litter decomposition in fragmented semi-arid forests, and none within the dry season in which most litter is shed. In this study, we employed litterbags filled with a common substrate to assess forest size and invertebrate detritivore effects on decomposition. Our results showed an average 14% litter mass loss along 3–9 months of incubation in the dry season, with variations being independent of forest size. Although exclusion resulted in slightly lower abundance of invertebrate detritivores, litter decomposition was similar in exclusion and non-exclusion treatments. We found no significant relationships between fragment size and invertebrate abundance or richness, which in turn did not influence decomposition. Temperature or moisture limitations, and even photo-degradation, could have masked differences in decomposition rates related to forest size during the dry season in semi-arid Chaco Serrano. Additionally, harsh environmental conditions during the incubation period could constrain the impact of invertebrate detritivores on the decomposition process. The absence of clear links between forest fragmentation, decomposition and soil fauna during the dry season, when conditions might be particularly limiting for this process, and when invertebrates could be expected to play a particularly important role, opens up new questions and highlights the complexity of this fundamental ecosystem process.

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1. Introduction

Forest loss is a main driver of the current biodiversity crisis affecting not only species composition, abundance and richness of biological assemblages (Cagnolo et al., 2009) but also altering ecosystem processes such as litter decomposition (Bennet and Saunders, 2010), which determines carbon turnover and nutrient cycling. At local scale, litter decomposition is influenced mainly by litter quality, microclimatic conditions and soil organisms (Gonzalez and Seastedt, 2001), all of which can be altered by forest size in fragmented landscapes. In smaller forest fragments, the

proportion of edge habitat increases leading to overall microclimatic conditions similar to those of edge habitats, i.e. higher light incidence, higher temperature and lower humidity, in comparison with larger fragments (Saunders et al., 1991). These particular microclimatic conditions could, in turn, affect litter quality via changes in plant community composition and both, microenvironment and litter quality alterations, could influence abundance, composition and activity of soil fauna (Vasconcelos and Laurance, 2005). Moreover, decreasing fragment size may lead to reduced plant and animal population size and increased risk of local extinctions (Ewers and Didham, 2006).

In semi-arid areas, moisture limitations for microorganisms may enhance the role of soil macro and mesofauna on litter decomposition (Araujo et al., 2012). However, most studies about forest fragmentation and soil fauna effects on leaf litter decomposition have been conducted in tropical forests (e.g. Vasconcelos and Laurance, 2005; Didham, 1998), with fewer studies from arid and

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semi-arid regions (Gonzalez and Seastedt, 2001; Xin et al., 2012). To our knowledge this is the first study from a seasonally dry forest focusing on the relationship between decomposition and forest area mediated by soil fauna within the dry season when most litter reaches the soil and when climatic conditions differ most from those of tropical and temperate forests.

Chaco Serrano is a seasonally dry subtropical forest from Central Argentina which lost over 90% of its original cover in recent years (Zak et al., 2004). In this ecosystem, fragmentation has resulted in biodiversity impoverishment, including plant and insect communities (Cagnolo et al., 2009), as well as alterations in ecological processes such as herbivory, parasitism (Valladares et al., 2006) and litter decomposition in the wet season (Moreno et al., 2014). In this study, we assessed the effects of fragment size and invertebrate detritivores on litter decomposition during the dry season in semi-arid Chaco Serrano. We expected that: (1) litter decomposition would be greater in larger than in smaller fragments; (2) abundance and richness of invertebrate detritivores would decrease with fragment size, showing changes in taxonomic composition due to differential vulnerability; (3) if invertebrate detritivores have a relevant impact on litter decomposition, their exclusion would significantly decrease litter decomposition rates, and such rates would be related to detritivore abundance, richness and/or taxonomic composition.

2. Materials and methods

The study was conducted in a fragmented area of Chaco Serrano in central Argentina (31°10' to 31°30'S and 64° 00' to 64°30'W). The region has a temperate climate with markedly scarce precipitations in winter. During the 9-month duration of the study, monthly mean temperatures ranged from 9.4 °C to 22.9 °C, with an accumulated rainfall of 362 mm and with water stress conditions along most of the incubation period (Fig. 1).

Native vegetation is currently restricted to isolated forest fragments within an intensely managed agricultural and urban matrix (Zak et al., 2004). We selected 12 of those fragments ranging from 0.57 ha to more than 1000 ha, keeping isolation between them (342.30 ± 90.56 m average distance to the nearest larger fragment) and matrix characteristics (soybean crop) as uniform as possible.

To analyze the effect of forest size on leaf litter decomposition we incubated, in all the selected sites, a common plant substrate (leaves of *Platanus acerifolia* (Ait.) Willd.) in order to control for litter quality effects (Berg and Laskowski, 2006). We collected leaf

litter in autumn, keeping it air-dried until processing. We prepared 216 litterbags (15 × 20 cm) with 0.3 mm mesh at the bottom (to avoid losing material from inside the bags) and 1 mm mesh on top, to prevent colonization by soil macroinvertebrates (e.g. ants, beetles, Diplopoda) and mesofauna (larger-bodied Acari and Collembola) while allowing microfauna access. On half of the litterbags, we made five 1-cm² perforations to facilitate soil fauna access (Vasconcelos and Laurance, 2005), in order to evaluate the effect of invertebrates on decomposition by comparing perforated and non-perforated litterbag decomposition patterns.

In February 2009, we placed nine perforated (non-exclusion treatment) and nine non-perforated (exclusion treatment) litterbags, each filled with 2 g of the common substrate, within each of the twelve forest fragments (in a 3 × 2 array with 1 m spacing, at approximately 20 m from the forest edge), covering them with local litter to simulate the natural decomposition conditions. After three, five and nine months of incubation, we randomly retrieved three perforated and three non-perforated litterbags of each fragment to determine litter decomposition in the period. Litterbags retrieved after three and five months of incubation were stored at 20 °C until processing (Vasconcelos and Laurance, 2005). Litterbags removed after nine months of incubation were first transported to the laboratory and their contents were placed in Berlese funnels (44 cm height, 20 cm diameter) under 60-W light bulbs during 7 days, for invertebrate extraction. The invertebrates were preserved in 70% ethanol solution. Finally, we cleaned and oven-dried the litter at 50 °C, during three days, to measure dry mass loss due to decomposition.

To estimate true dry mass we first calculated air-dried water content. We air-dried a subsample of the common substrate and then oven-dried it at 50 °C until constant weight was achieved (about 48 h). Water content (%) was calculated from the mass loss in samples after drying. As litterbags can be contaminated with soil, we also corrected litter mass loss as the effective loss of organic matter (litter mass loss without ashes) by burning the samples in an oven at 500 °C for 4 h (Perez Harguindeguy et al., 2013). We calculated the decomposition constant (k -value) as follows: $k = -\ln(M_t/M_0)/t$, where k = decomposition rate constant (year⁻¹), M_0 = mass of litter at time 0, M_t = mass of litter at time t , and t = duration of incubation (years) (Perez Harguindeguy et al., 2013).

All specimens extracted from litterbags were counted and identified (to Family level in the case of insects and to Order level for other invertebrates) and assigned to detritivore or other functional groups depending on the dominant feeding habit of each taxonomic group. We performed all statistical analyses using detritivores only.

We expressed litter decomposition rates as the percentage of dry mass loss per litterbag, whereas abundance and richness of invertebrate detritivores were indicated by the number of individuals or taxa per litterbag. To evaluate the effects of fragment size on (a) litter decomposition rates and (b) detritivore abundance and richness, we used (a) a linear mixed-effects model (LMM) and (b) generalized linear mixed models (GLMM) with litter decomposition rate, abundance or richness as response variables, fragment area (log+1-transformed to linearize the relationship) and exclusion treatment as fixed effects, and site (forest fragment) as random effect. In (a) we also incorporated incubation time as fixed effect and, nested within site, as random effect in order to contemplate dependence of repeated measurements over time. Litter decomposition and abundance-richness were fitted with a Gaussian and a Poisson error structure, respectively. We performed a principal component analysis (PCA) to explore changes in taxonomic composition (quantitative data) of invertebrate assemblages, using the software Infostat version 2008. We employed Spearman correlations between assemblage position on each of the two first

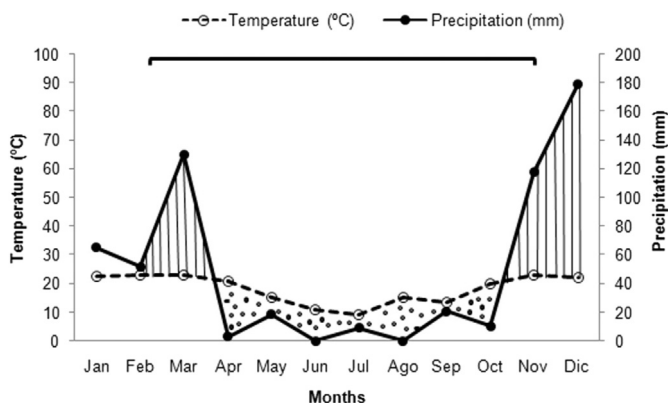


Fig. 1. Climograph of the study site, mean values January to December 2009. JAN = January, FEB = February, MAR = March, APR = April, MAY = May, JUN = June, JUL = July, AUG = August, SEP = September, OCT = October, NOV = November, DEC = December. Bracket on the top indicates the study period. The dotted areas indicate periods of water stress and the striped areas indicate periods of excess water.

PCA axes vs fragment area and decomposition rates, in order to assess relationships between these factors and community taxonomic structure. We used linear mixed-effects models to analyze the influence of detritivore abundance and richness on litter decomposition, with decomposition rate as response variable, abundance and richness as fixed-effects and site (forest fragment) as random effect. Non-significant interactions between fixed effects were removed in order to obtain the most parsimonious model. We performed statistical analyses using the software R 2.11.0 (R Development Core Team, 2010).

3. Results

Litter decomposition did not show significant differences between incubation periods (Table 1, Fig. 2a and see Fig. S1 for decomposition dynamics). The decomposition constant (k -value) obtained during the incubation period was, on average, $k = 0.20$. Litter mass loss was independent of forest area (Table 1, Fig. 2a), and no significant interaction was detected between forest area and time (Table 1).

In total, we collected 1232 specimens from 43 taxa. Each litterbag provided, on average, 15.2 (± 1.3) specimens from 4.3 (± 0.2) taxonomical groups. From a functional point of view, most of the specimens collected (90%) were detritivores (Fig. S2). The detritivore assemblages were represented by 22 taxa and were numerically dominated by snails (Stylomatophora) and ants (Hymenoptera: Formicidae) which together accounted for 70.2% of total detritivore abundance in both exclusion and non-exclusion bags.

We found no differences in detritivore richness between exclusion and non-exclusion treatments (Table 1, Fig. 3b1). Although there was a significant effect of exclusion treatment on detritivore abundance (Table 1, Fig. 3a1), we found only 8% fewer detritivores in exclusion treatment compared to non-exclusion treatment. Both detritivore abundance and richness were independent of forest area (Table 1, Fig. 3a–b), without significant interactions between forest area and exclusion/non-exclusion treatment (Table 1). The taxonomic composition of the invertebrate

assemblages showed no clear trend in the degree of similarity between fragments of different size (PCA, Fig. S3), which was corroborated by the lack of correlation between either of the two main PCA axes and fragment size (PC1: $r = 0.21$, PC2: $r = 0.49$, $p > 0.05$ in both cases).

Litter decomposition rates did not differ between exclusion and non-exclusion litterbags (Table 1, Fig. 2a1). Moreover, no significant interaction was detected between forest area and treatment, or treatment and time (Table 1). Finally, mass loss of the common substrate was independent of detritivore abundance, richness (Table 1, Fig. 2b–c) and taxonomic composition, the latter indicated by non-significant Pearson correlations with PCA values (PC1: $r = 0.51$, PC2: $r = 0.13$, $p > 0.05$).

4. Discussion

In what is, to our knowledge, the first study of litter decomposition during the dry season in a fragmented seasonally dry forest, we found that the size of Chaco Serrano fragments did not affect either common substrate decomposition or invertebrate detritivore assemblages (abundance, composition or richness). Our results also showed that invertebrate detritivores did not influence the decomposition process during the dry season at Chaco Serrano fragments.

Litter decomposition in Chaco Serrano reached nearly 14% mass loss after the initial incubation phase, but did not vary between three, five or nine months of incubation. The initial decomposition phase coincided with a precipitation peak (see Fig. 1), after which a persistent water stress period and consequently low soil humidity, added to low temperature, could have hindered litter decomposition. However, the decomposition rates here recorded after nine months of incubation were rather similar to the values (4–18%) observed over a four month period of dry summer in Mediterranean systems (Dirks et al., 2010). Also, decomposition constants similar to those we obtained in central Argentina ($k = 0.2$) have been recorded from other semi-arid systems as in central Queensland (Australia) where decomposition constants ranged from 0.17 to 0.38 (Sangha et al., 2006), and northeastern China with

Table 1
Relationships between litter decomposition, soil fauna and forest size. Results from linear mixed models for decomposition rates and generalized linear mixed models for invertebrate abundance and richness. Time: incubation period (3, 5 and 9 months). Treatment: Exclusion or Non-exclusion of invertebrate detritivores. Data from three litterbags per treatment and incubation period in each of 12 forest fragments. Only data from the 9-month incubation period were used for analyses including invertebrate abundance and richness.

Response variable	Explanatory variable	Statistic	p	StdDev	Residual StdDev
Decomposition rate	Forest area	F = 0.03	0.858		
	Time	F = 0.65	0.533		
	Treatment	F = 3.46	0.065		
	Forest area: Time	F = 1.04	0.356		
	Forest area: Treatment	F = 0.74	0.392		
	Treatment: Time	F = 0.84	0.435		
	Random effects				
	Site/Time			0.571	5.697
	Invertebrate abundance	F = 3.12	0.083		
	Invertebrate richness	F = 3.18	0.080		
Invertebrate abundance	Random effects				
	Site			3.735	4.484
	Treatment	$\chi^2 = 7.08$	0.008		
	Forest area	$\chi^2 = 0.30$	0.584		
	Forest area: Treatment	$\chi^2 = 1.91$	0.167		
Invertebrate richness	Random effects				
	Site			0.334	
	Treatment	$\chi^2 = 1.77$	0.184		
	Forest area	$\chi^2 = 1.65$	0.200		
	Forest area: Treatment	$\chi^2 = 0.04$	0.836		
	Random effect				
	Site			3.211e-06	

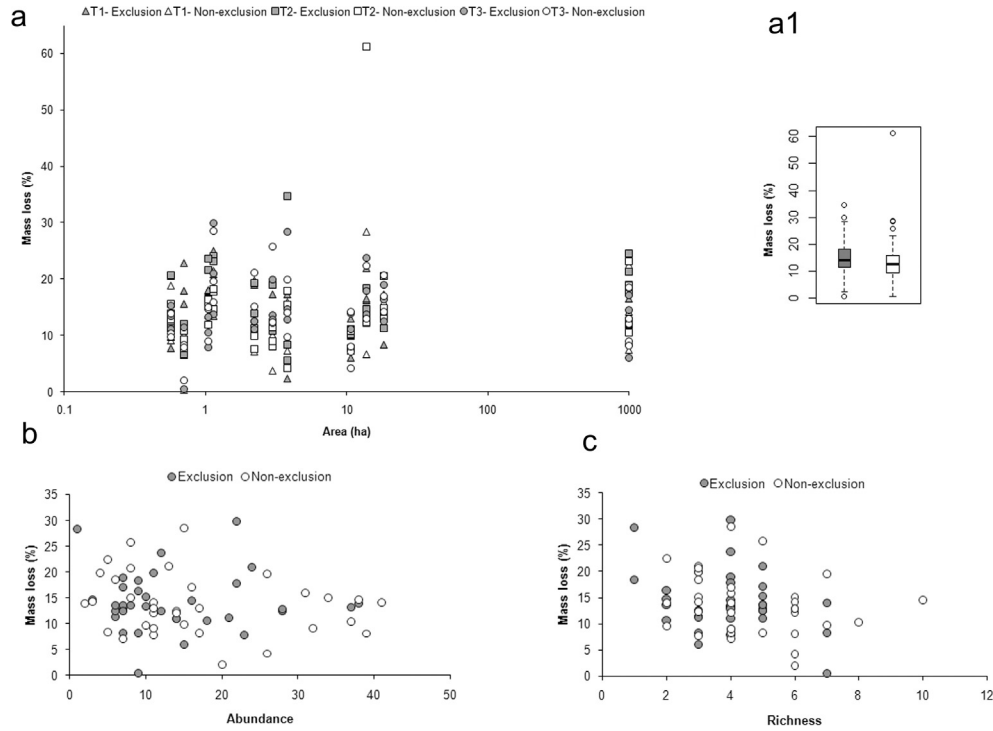


Fig. 2. Litter decomposition rates along a size gradient of Chaco Serrano fragments, in relation to a) forest area, b) invertebrate detritivore abundance and c) invertebrate detritivore richness in exclusion and non-exclusion treatments. Box plot on the right (a1) shows average litter decomposition in exclusion and non-exclusion treatments. In panel a, T1, T2 and T3 correspond to incubation periods (three, five and nine months respectively).

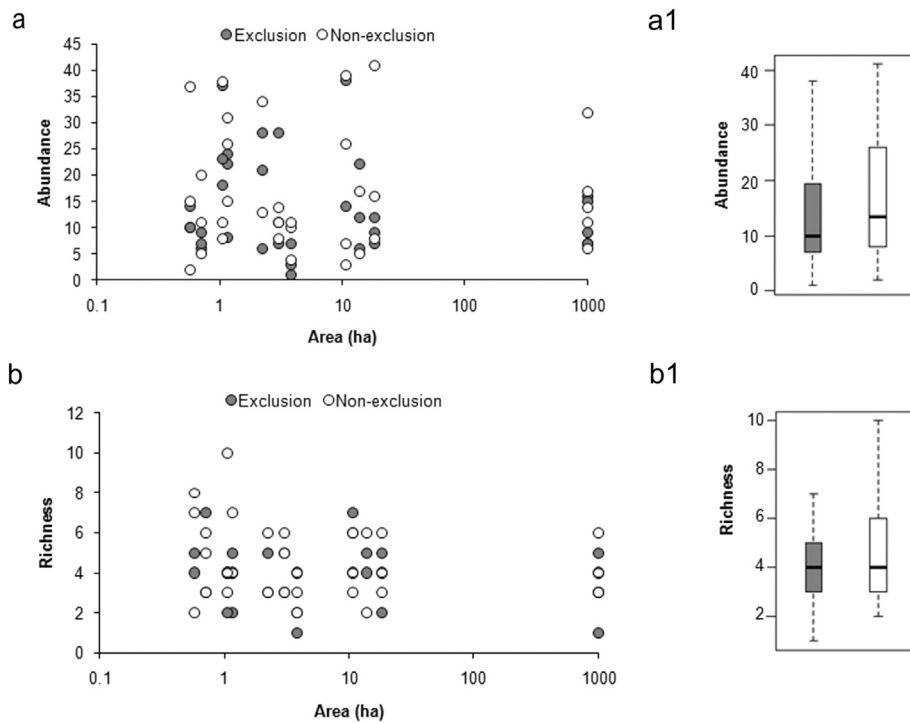


Fig. 3. Relationships between fragment size and a) abundance, b) richness of invertebrate detritivores in exclusion and non-exclusion treatments. Box plots on the right illustrate average a1) abundance and b1) richness of invertebrate detritivores in exclusion and non-exclusion treatments.

k values from 0.21 to 0.29 (Xin et al., 2012).

Although litter decomposition of the common substrate showed four-fold variations among forest fragments, such changes were not

related to forest fragment size. This result is coincident with those found in other studies including an Andean wet forest in Colombia (Varela et al., 2002), a temperate woodland of Australia (Hastwell

and Morris, 2013) and a tropical forest in Brazil (Vendrami et al., 2012). Contrastingly, for the latter system other experiments did show lower litter decomposition rates in smaller fragments (Didham, 1998). Also, a recent work within the same study area of the present study (Moreno et al., 2014) found lower decomposition of a common substrate in smaller fragments, during the wet and warm summer season. In general, the idiosyncrasy in findings, even within the same study area, suggests that the effects of fragment size on decomposition may be context dependent. In our study, temperature and moisture limitations (see Fig. 1) could have attenuated litter decomposition patterns during the dry season in fragmented Chaco Serrano. Other factors could also be involved, such as photodegradation, an important control of litter decomposition in water-limited ecosystems due to its influence on litter chemical composition and microbial community characteristics (Austin and Vivanco, 2006; Mlambo and Mwenje, 2010). Photodegradation is expected to be more pronounced in smaller fragments, where a diminished vegetation cover intercepts a lesser portion of the incoming solar radiation in comparison with larger fragments, but differences in interception may fade during the dry season when most species lose their foliage. Thus a generalized intensification of photodegradation could offset the relationship between litter decomposition rates and forest size observed by Moreno et al. (2014).

With 15 specimens in more than four taxonomic groups per litterbag, the soil fauna in Chaco Serrano showed relatively high abundance and diversity during the dry season in comparison to other semi-arid systems. For example, in semi-arid regions of China (Xin et al., 2012) only 1 to 3 individuals were collected in each litterbag analysed, whereas a study conducted in Patagonia, Argentina (Araujo et al., 2012) reported an average of 4 individuals per litterbag. The relatively abundant invertebrate detritivore assemblages found within litterbags in Chaco Serrano appeared to be insensitive to forest fragment size during the dry season, without effects either on abundance, richness or composition. Likewise, lack of fragment size effects has been reported for other decomposition-related groups, e.g. leaf-litter beetles (Didham, 1998), leaf-cutter and fungus-growing ants (Lozano-Zambrano et al., 2009). Fragment size effects might be conditioned by the way each organism perceives its environment (Chust et al., 2003). In Chaco Serrano fragments, predominantly small body sized invertebrates, with generalist feeding habits, may perceive a small volume of soil as a habitat full of resources and thus might be able to persist, unaffected, even in small fragments.

We found that neither abundance nor richness or taxonomic composition of invertebrate detritivore communities affected litter decomposition in Chaco Serrano across fragments. This could result from the adverse climatic conditions of the incubation period, with low temperatures and scarce precipitations, which probably may have constrained the impact of invertebrate detritivores on the decomposition process (Araujo et al., 2012) in semi-arid Chaco Serrano. Our exclusion experiment did not contribute to clarify the relationship between invertebrates and decomposition, because of the small magnitude of the difference in detritivore abundance between exclusion and non-exclusion bags. Additionally, it may be not species number but functional dissimilarity among detritivore species what drives decomposition (due to facilitative interactions among species), as has been proposed in relation to other ecosystem processes (Heemsbergen et al., 2004). In our study, detritivores were represented mainly by macrofauna (e.g. ants, snails, beetles), which consume and break up organic material (Vasconcelos and Laurance, 2005). The scarce representation of mesofauna (Acari, Collembola and Psocoptera), highly dependent on moisture, may have limited decomposition via trophic interactions with the microbial community. Studies in arid and semi-

arid ecosystems found that mass loss was regulated by predatory mites preying on bacteriophagous nematodes; when predatory mites decreased in number, nematodes increased exponentially and overgrazed the fungi and bacteria, reducing rates of litter decomposition (Elkins and Whitford, 1982). However, Austin and Vivanco (2006) found that inhibiting fungal and bacterial activity via biocide application had no effect on litter decomposition in a semi-arid ecosystem in southern Argentina.

Summing up, our results have shown that variations in decomposition of a common substrate among forest fragments in Chaco Serrano during the dry season could be explained neither by changes in the invertebrate detritivore assemblages, nor by the size of the forest fragments. In addition to temperature or moisture limitations, other factors such as photodegradation could be masking forest size influences on the decomposition process during the dry season in semi-arid Chaco Serrano. The absence of clear links between forest fragmentation, decomposition and soil fauna during the dry season, when conditions might be particularly limiting for this process, and when invertebrates could be expected to play a particularly important role, opens up new questions and highlight the complexity of this fundamental ecosystem process.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2015.11.009>.

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