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Edge and herbivory effects on leaf litter decomposability in a subtropical dry forest

Abstract It is increasingly recognized that understanding the functional consequences of landscape change requires knowledge of aboveground and belowground processes and their interactions. For this reason, we provide novel information addressing insect herbivory and edge effects on litter quality and decomposition in fragmented subtropical dry forests in central Argentina. Using litter from *Croton lachnostachyus* (a common shrub species in the region) in a decomposition bed experiment, we evaluated whether litter quality (carbon and nitrogen content; carbon: nitrogen ratio) and decomposability (percentage of remaining dry weight) differ between litter from forest interiors or edges (origin) and with or without herbivory (damaged/undamaged leaves). We found that edge/interior origin had a strong effect on leaf litter quality (mainly on carbon content), while herbivory was associated with a smaller increase in nitrogen content. Herbivore damage increased leaf litter decomposability, but this effect was related to origin during the initial period of litter incubation. Overall, undamaged leaf litter from the forest edge showed the lowest decomposability, whereas damaged leaf litter decomposed at rates similar to those observed in litter from the forest interior. The interacting edge and herbivory effects on leaf litter quality and decomposability shown in our study are important because of the increasing dominance of forest edges in human-modified landscapes and the profound effect of leaf litter decomposition on nutrient cycling.

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Introduction

Worldwide deforestation and fragmentation have led to an increase in artificial forest boundaries (Harper et al. 2005; Riutta et al. 2014), which tend to have abrupt edges characterized by biotic and physical traits that clearly differ from those at the forest interior. Such edge conditions, arising mainly from increased solar radiation and wind exposure, frequently have harsher and more extreme microenvironmental conditions than those of natural boundary areas (Didham and Lawton 1999; Bergès et al. 2013). These changes in forest edge conditions, together with corresponding changes in species number and community composition (Harper et al. 2005) may affect ecosystem processes (Fagan et al. 1999; Martinson and Fagan 2014).

Leaf litter decomposition is a fundamental process for the recycling of carbon and nutrients in terrestrial ecosystems (Chapin 2002; Austin and Vivanco 2006). The main factors regulating this process are environmental conditions (primarily moisture and temperature; Coûteaux et al. 1995), plant litter quality (Cornelissen 1996; Pérez-Harguindeguy et al. 2013) and the biotic community (Gonzalez et al. 2001; Meyer et al. 2011). At forest edges, increased radiation from the sun, higher temperatures and lower humidity (Saunders et al. 1992; Chen et al. 1999) may affect how decomposition occurs and trigger changes in this process through various mechanisms. Some previous studies have examined the edge influence on decomposition via changes in microclimate and soil communities (e.g. Didham 1998; Riutta et al. 2012), but few have addressed leaf litter quality as a potential mechanism mediating edge effects (Vasconcelos and Laurance 2005; Romero-Torres and Varela Ramirez 2011). Indeed, edge microclimatic conditions can alter physical and chemical leaf attributes (Ishino et al. 2012). For example, higher radiation from the sun

increases leaf carbon content and the carbon: nitrogen (C:N) ratio (Henriksson et al. 2003; Muth et al. 2008). Such leaf attributes may persist in litter and affect its decomposability (Pérez-Harguindeguy et al. 2000). Changes in plant community composition at forest edges (Laurance et al. 1998; Vasconcelos and Laurance 2005) can also alter litter quality and decomposability, particularly with changes in the relative abundance of different functional types of plants (Laurance and Curran 2008).

Decomposition may also interact with aboveground processes like herbivory. Herbivore damage can accelerate leaf litter decomposition via mechanical fragmentation and the fall of green foliage material ("greenfall", e.g. Schowalter et al. 2011) or by inducing premature foliar abscission, thus interrupting reabsorption of nutrients and leading to N-rich litter (Hunter 2001; Chapman et al. 2003; Mazía et al. 2012). Damage by insect herbivores can also weaken the physical leaf structure and increase its contact surface for microbiota involved in decomposition (Cárdenas and Dangles 2012). Alternatively, secondary compounds such as polyphenols or terpenes may increase following leaf damage (Van der Putten et al. 2001; Agrawal 2011) and, if these compounds persist in leaf litter (Hunter 2001; Chapman et al. 2006), they may slow decomposition (Findlay et al. 1996). Nonetheless, to our knowledge, changes in litter quality associated with herbivory have not yet been explored in relation to edge effects. Thus, the present study offers new information regarding the interactions between aboveground and belowground ecological processes by considering a canopy process (herbivory) and a soil process (litter decomposition) in edge/interior locations.

Here, we aim to improve our understanding of the decomposition process in fragmented subtropical dry forests in central Argentina (Moreno et al. 2014). We will carry this out by addressing how herbivory and edge effects mediated by changes in leaf litter quality affect the decomposability of the abundant plant species *Croton lachnostachyus* Baill. We expect leaf litter from forest edges will have lower quality (high C content and high C:N ratio) and decomposability compared with litter from the interior, because of the drier and more extreme microclimatic conditions at the forest edge. Additionally, we expect litter with herbivore damage to be associated with either increased decomposition (resulting from mechanisms like nutrient resorption, physical debilitation) or decreased decomposition (resulting from induced defences).

Materials and methods

Study area and species selection

The study was conducted within the Chaco Serrano District in Central Argentina. The average annual rainfall in the region is about 750 mm, and is concentrated in the warm season (October–pril). The maximum and minimum temperatures in the district are 26 and 10 °C, respectively. The characteristic vegetation is low, open woodland, currently reduced to isolated remnants embedded in a predominantly agricultural matrix (Zak et al. 2004).

The plant species selected to evaluate changes in leaf litter quality and decomposability was *Croton lachnostachyus* (Euphorbiaceae), a native perennial shrub (0.7–2 m tall) that is common in the region (Sérsic et al. 2006). This species was suitable for our study objectives because (1) it is abundant both at the interior and at the edge of most forest fragments; (2) its leaves are consumed by several groups of insects, including leaf miners, chewers and sap-suckers (Rossetti et al. 2014); and (3) its litter decomposes rapidly (Pérez-Harguindeguy et al. 2000) allowing trends to be detected in a relatively short period of time.

Litter collection and treatments

We collected freshly senesced *C. lachnostachyus* leaf material during the peak of leaf fall (May–July 2010) from 10 to 15 individuals at the forest edge (within 2 m from the outer tree line) and interior (approximately 25 m from the tree line) in each of five woodland remnants (9.85–1000 ha) and transported them in paper bags. At the laboratory, we thoroughly mixed the five collections from the interior together and the five collections from the edge to form two pools (interior and edge). From these pools, we carefully separated out herbivore-damaged litter (mainly by chewing insects) and undamaged litter. Thus, we obtained four groups: edge-damaged, edge-undamaged, interior-damaged and interior-undamaged leaf litter. All litter was then air-dried. We constructed litterbags for each group and used three subsamples to determine initial leaf litter quality.

For the three subsamples from each group, we estimated initial total carbon (C) as 50% of ash-free biomass (Gallardo and Merino 1993). Initial total nitrogen (N) was measured with an autoanalyser (RFA 300-Alpken; Wilsonville, OR, USA) at the chemical analysis laboratory of the Instituto Nacional de Tecnología Agropecuaria (INTA) Bariloche. The C:N ratio was the calculated from these data.

Using 20 subsamples from each group, we constructed 20 litterbags (10 replicates for each retrieval date; a total of 120 litterbags) of 10×15 cm with 0.3-mm nylon mesh on the bottom side and 1-mm nylon mesh on the upper side. The smaller mesh prevents litter loss from the bottom, and the coarser mesh allows access to micro and mesofauna through the top of the bag. We filled each litterbag with 2 ± 0.02 g of *C. lachnostachyus* leaf litter. To estimate the true initial dry mass, we first calculated air-dried water content by air-drying five subsamples of the leaf litter substrate and then oven-drying

them at 60 °C for 48 h. The water content (%) was deducted from the air-dry mass in all samples.

In April 2011, all the litterbags were labeled and randomly placed in a decomposition bed in the largest of the five woodland remnants. Before burial, the top 5 cm of soil was removed and the bed was mixed with soil collected from the same continuous site. In all cases, the smaller-mesh side was in contact with soil, and the larger-mesh side was covered with natural litter to simulate natural decomposition conditions. We retrieved 10 litter bags per group after 120 and 240 days of incubation, transported them in paper bags to the laboratory, and stored them at −4 °C until processing. Samples were then defrosted, gently cleaned by removing any exogenous material, and oven-dried at 60 °C for 48 h to determine their dry mass. We estimated decomposability as the percentage of remaining dry weight (% RDW) from the difference between the initial litter dry weight and dry weight after the incubation period.

Data analysis

We evaluated whether litter quality (model 1) and decomposability (model 2) differed in leaf litter from different origins (edge/interior) and in leaf litter with or without herbivore damage (damaged/undamaged) using linear models (Pinheiro and Bates 2000). Model 1 included C content, N content and C:N ratio as response variables, with litter origin (edge/interior) and herbivory (damaged/undamaged) as fixed effects. In model 2, decomposability (% RDW) was the response variable and the same fixed effects were used as in model 1 (origin and herbivory). For this, we used a generalized linear model with binomial distribution and a logit link function, which was performed separately for each incubation period (120 and 240 days). We evaluated the interactions between the fixed effects (origin and herbivory) in all models. We also explored the relationship between leaf litter decomposability (for both incubation periods) and leaf litter quality by performing Spearman correlation analysis on litterbag decomposability versus initial quality (C, N or C:N) in each group. Before running the models, the assumptions of the linear and generalized linear models were checked. Statistical analyses were performed using the software R 3.2.2 (R Development Core Team 2015), with significance at $P \leq 0.05$.

Results

The initial carbon content of *C. lachnostachyus* leaf litter was significantly affected by litter origin and was associated with herbivory only for leaves from edge habitats (significant herbivory × origin) (Table 1; Fig. 1). Leaf litter from forest edges had 2% higher C content than litter from the interior. Within litter from forest edges, C content was 1% lower in herbivore-damaged than undamaged leaf litter (Fig. 1a). Both origin and herbivory significantly affected initial N content and C:N ratio (Table 1). N content was 7% higher in damaged than undamaged leaf litter and 8% higher in leaf litter from the forest edges in than that from the interior (Fig. 1b). The C:N ratio was 8% lower in damaged than in undamaged leaf litter and 7% higher in samples from the forest interior than those from the edges (Fig. 1c).

Approximately 70% of *C. lachnostachyus* leaf litter mass remained after 120 days of incubation (range = 54–89%) and about 63% mass remained after 240 days (range = 50–79%). Leaf litter decomposability differed according to litter origin and herbivore damage, but the effects depended on time of incubation (Table 2; Fig. 2). For the shorter incubation period (120 days), leaf litter decomposability was significantly influenced by litter origin, herbivory and their interaction, with undamaged leaf litter from the forest edge (characterized by the highest C content and C:N ratio; Fig. 1) showing the lowest decomposability (highest % RDW; Table 2; Fig. 2). After 240 days, only herbivore damage had a significant effect on decomposability (Table 2); that is, damaged leaf litter (characterized by higher N and lower C:N ratio; Fig. 1) decomposed faster (lower % RDW; Fig. 2) than undamaged leaf litter. When decomposability was plotted against initial litter quality, the only significant relationship was observed at 240 days, when % RDW increased with increasing C:N ratio ($R = 0.41$;

Table 1 Results of linear models examining the effects of herbivory (damaged/undamaged leaves) and origin (edge/interior) on carbon, nitrogen and carbon: nitrogen ratio in *Croton lachnostachyus* leaf litter

	Explanatory variables	df	F	P
C content (%)	Origin	**1, 8**	**92.57**	**< 0.0001**
	Herbivory	1, 8	3.17	0.11
	Herbivory × origin	**1, 8**	**8.13**	**0.02**
N content (%)	Origin	**1, 8**	**11.33**	**0.01**
	Herbivory	**1, 8**	**6.97**	**0.03**
	Herbivory × origin	1, 8	0.43	0.53
C:N ratio	Origin	**1, 8**	**6.62**	**0.03**
	Herbivory	**1, 8**	**8.73**	**0.02**
	Herbivory × origin	1, 8	0.34	0.57

Letters in bold indicate significant effects ($P < 0.05$)

Table 2 Results of generalized linear models examining the effects of herbivory (damaged/undamaged leaves) and ha origin (edge/interior) on decomposability (percentage of remaining dry weight) of *Croton lachnostachyus* leaf litter after two incubation periods

Explanatory variables	df	Z	P
120 days			
Origin	**1, 33**	**−2.38**	**0.017**
Herbivory	**1, 33**	**−5.84**	**< 0.001**
Herbivory × origin	**1, 33**	**5.42**	**< 0.001**
240 days			
Origin	1, 33	−0.41	0.681
Herbivory	**1, 33**	**−3.33**	**< 0.001**
Herbivory × origin	1, 33	1.21	0.237

Letters in bold indicate significant effects ($P < 0.05$)
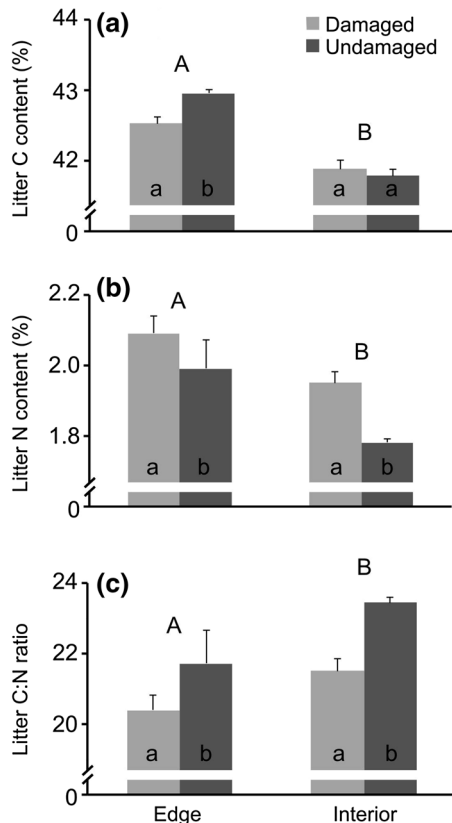
Fig. 1 Initial litter quality (average ± SE) as indicated by C content (%) (**a**), N content (%) (**b**) and C:N ratio (**c**) of damaged (*light gray bars*) and undamaged (*gray bars*) leaf litter of *C. lachnostachyus* plants from forest interior and edge locations. *Different uppercase letters* indicate significant differences between interior/edge leaves; *different lowercase letters* indicate significant differences between damaged/undamaged leaves

$P = 0.01$), indicating a negative relationship between decomposability and C:N ratio.

Discussion

In this study, we have shown that leaves from the forest edge and undamaged leaves were associated with lower leaf decomposability, which was partially explained by
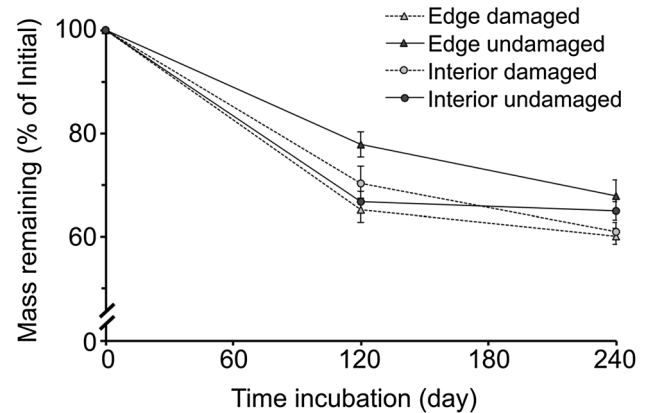
Fig. 2 Decomposability (% remaining dry weight, average ± SE) of damaged/undamaged leaf litter of *C. lachnostachyus* from forest interior and edge locations

variations in leaf litter quality. These results are particularly relevant in the context of increasing forest fragmentation worldwide. Despite a long history of research on edge effects, there is a lack of knowledge about decomposition responses to edge effects through litter quality and its interplay with leaf herbivory.

In the current study, edge effects had the greatest influence on C content. This is surprising because C is known to vary relatively little between species and much less within species (Pérez-Harguindeguy et al. 2013 and literature cited therein). The higher C content in *C. lachnostachyus* leaf litter collected from forest edges may be attributable to higher radiation from the sun, a phenomenon frequently associated to edge habitats (Murcia 1995). The magnitude of variation in C content between edge and interior habitats that we found (2%) closely resembles results from experimental studies comparing leaves from plants grown in sunlight versus leaves from plants grown in the shade (a ~3% difference in C; Barber and Marquis 2011; Stoepler and Rehill 2012). The higher C content in leaves from the forest edge was not accompanied by lower N content as found in previous studies (e.g. Barber and Marquis 2011). On the contrary, we found that leaves from the edge had slightly higher N content than those from the interior. The leaves of woody species growing in sunlit environ-

ments are expected to have about 15% less N than leaves growing in shade (Barber and Marquis 2011; Stoepler and Rehill 2012). However, light exposure may produce the opposite pattern in shrubs, like the species used in our work (e.g. Karolewski et al. 2013), via increased photosynthesis (Roberts and Paul 2006 and literature cited therein).

Herbivore damage was associated with higher N content and lower C:N ratio in leaf litter. This may be explained by premature leaf abscission and incomplete nutrient reabsorption leading to N-rich litter in damaged leaves (Hunter 2001; Chapman et al. 2006; Zvereva and Kozlov 2014) or it might be a result of herbivores choosing high-quality leaves, a process widely reported in the literature (e.g. Mattson 1980; Schädler et al. 2003). Although we cannot rule out the latter possibility, some evidence from the same study area and on the same plant species suggests that herbivores are not selecting high-N content leaves in this system. In a previous work, leaves from the forest edge had higher N content but lower herbivory than those in the interior (Rossetti et al. 2014).

Leaf litter decomposability was only associated with the C:N ratio after 240 days of incubation. Previous studies have pointed at the C:N ratio as a good predictor of leaf litter decomposition (Enriquez et al. 1993; Pérez-Harguindeguy et al. 2000; Cortez et al. 2007), with higher decomposition in litter with lower C:N ratios. However, there is evidence that decomposition dynamics could be better predicted by combinations of different recalcitrant litter compounds than by single litter traits (Vaieretti et al. 2005; Kurokawa and Nakashizuka 2008). Moreover, a decrease in litter C:N ratio was linked to herbivory in our study, suggesting increased leaf litter decomposability. Interestingly, this effect depended on litter origin during the initial period of incubations. That is, undamaged leaf litter from the forest edge showed the lowest decomposability (highest % RDW), while its herbivore-damaged counterpart decomposed at the lowest rate. Although, a recent study showed no effects of herbivore damage on subsequent leaf litter decomposition (Cárdenas et al. 2015), herbivory of *C. lachnostachyus* appears to facilitate the decomposability of low-quality leaf litter from forest edges.

In summary, our results suggest complex interactions involving edge effects and aboveground as well as belowground processes; the edge effect may diminish the rate of leaf litter decomposition, but the presence of herbivore damage appears to compensate for these negative effects. Studies at the plant community level and in different geographical settings are needed to evaluate the generality of the patterns observed for *C. lachnostachyus*. Furthermore, evaluation of a wider range of chemical traits may improve our understanding of the role of leaf litter quality. The current study highlights the need to consider the interactions between canopy processes and soil processes in fragmented landscapes where edge habitats may be dominant.

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