Short communication

Area and edge effects on leaf-litter decomposition in a fragmented subtropical dry forest

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ABSTRACT

South American subtropical dry forests are highly threatened by fragmentation. Despite considerable research efforts aimed at predicting ecosystem alterations due to this driver of global change, we still need to deal with general principles to improve our ability to predict the impact of fragmentation. Our work is one of the few studies that analyse the relationship between forest fragmentation and decomposition. In 12 remnants of Chaco Serrano forest in Central Argentina we tested if decomposition rates of a common leaf-litter substrate varied with fragment size and between the forest edge and interior. Decomposition declined with fragment size, with no significant effects of location (edge/interior) or interaction between the two components of fragmentation. Our results suggest that *in situ* conditions for decomposition may change as a consequence of forest fragmentation, specifically as a result fragment size. This may lead to impaired nutrient recycling in smaller forest remnants.

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1. Introduction

South American tropical and subtropical dry forests are disappearing at an alarming rate, with 80% deforestation of the original area being recorded in the last decade (Aide et al., 2013). Deforestation involves habitat loss and fragmentation leading to the transformation of a forested area to a number of smaller forest remnants embedded in a matrix with different land use, usually agricultural (Fahrig, 2003). Although ongoing habitat loss and fragmentation are recognized as primary drivers of contemporary extinctions (Brook et al., 2008), we still need to deal with general principles to improve our ability to predict the impacts of processes involved in land use change. In order to achieve this goal, information from field studies representing different ecosystems is a fundamental requirement.

There has been a long debate on the distinction between habitat loss and habitat fragmentation per se (Banks-Leite et al., 2010; Ewers and Didham, 2007; Haila, 2002). In a valuable attempt to reach a generalization, Fahrig (2003) showed that habitat loss had larger and consistently negative effects on biodiversity while different components of habitat fragmentation per se (e.g. isolation, edge effects, matrix quality) had weaker effects, which could be either positive or negative. Didham et al. (2012) proposed that in spite of the magnitude of each effect on biodiversity, they all operate through chains of direct and indirect causal links which should be addressed by fragmentation studies. How the different components of fragmentation alter ecosystem processes has not been studied extensively particularly in South American ecosystems (Grez and Galetto, 2011).

As forest remnants become smaller, they become increasingly dominated by edge habitat (Ries et al., 2004). Remnants edges can present particular microclimatic characteristics such as reduced humidity, greater temperature variability and increased solar radiation in comparison with the forest interior (Laurance, 2004). Consequently, smaller forest remnants, with a high proportion of edge habitat, may be, on average, hotter and drier compared to larger ones. However, microclimate changes between the edge and interior could be more complex (Davies-Colley et al., 2000; Gehlhausen et al., 2000), with even opposite trends in microclimatic factors being recorded (Wright et al., 2010). In spite of the intrinsic relationship between remnant area and edge/interior

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location, most studies focus either on the ecological responses to habitat loss or to edge effects.

Leaf-litter decomposition is a fundamental process that contributes to carbon and nutrient cycling and hence to ecosystem productivity (Hättenschwiler et al., 2005; Zhang and Zak, 1995). This process is hierarchically controlled by climatic conditions (e.g. temperature and humidity Coûteaux et al., 1995), leaf quality (Cornelissen et al., 1999) and soil organisms (Gonzalez and Seastedt, 2001). The relationship between habitat fragmentation and decomposition has been addressed in very few studies and the results reported have been inconclusive. For example, decomposition was slower at the edge in comparison with the interior of temperate mixed deciduous forests (Riutta et al., 2012), whereas in Andean cloud forests (Romero-Torres and Varela Ramírez, 2011) and Australian dry forests (Hastwell and Morris, 2013) the effects on decomposition depended on edge orientation. Similarly variable responses to edge conditions have been reported for tropical systems (Didham, 1998; Noble, 2013; Rubinstein and Vasconcelos, 2005). With regard to fragment size, different studies have found either a decline in decomposition with forest area (Didham, 1998; Wardle, 1997) or no effects (Hastwell and Morris, 2013; Noble, 2013; Rubinstein and Vasconcelos, 2005). We know of no study simultaneously addressing the effects of edge/interior location and fragment area on decomposition in subtropical dry forests, except for the work by Hastwell and Morris (2013) in which edge effects were thoroughly explored but area variations were represented by four forest fragments.

In this context, we experimentally analysed leaf-litter decomposition along an area gradient in a fragmented Chaco Serrano forest in central Argentina. This system is part of the most extensive and highly threatened dry forest in South America (Zak et al., 2004). We were interested in whether decomposition can be affected by forest area and edge effects. By using a common substrate (from native plants) we avoided effects mediated by changes in litter quality, thus focussing on effects of *in situ* conditions for decomposition.

2. Materials and methods

2.1. Study area

The study was conducted in the Chaco Serrano District, in central Argentina, a seasonally dry forest with a mean temperature of 17.5 °C and an average annual rainfall of 750 mm mostly concentrated in the warm season (October–April) (Fig. 1). The native vegetation, currently reduced to isolated remnants embedded in a predominantly agricultural matrix, includes a tree layer (8–15 m high), shrubs (1.5–3 m), herbs and grasses (0–1 m) and many vines and epiphytic bromeliads (Cagnolo et al., 2006). In an area located

between 31°10′–31°30′ S and 64°00′–64°30′ W, at 500–600 m a.s.l., twelve forest fragments which had been isolated for at least 30 years, ranging in size from 0.57 ha to over 1000 ha were selected.

2.2. Litter bag experiment

We collected freshly senesced leaf material of two abundant native species (*Celtis ehrenbergiana* (Klotzsch) Liebm. and *Croton lachnostachyus* Baill.) during the peak of leaf fall (May–August 2009), within the largest forest remnants (>1000 ha). We determined initial leaf-litter quality of those two common substrates (see Table 1). Samples of the two species were oven-dried at 50 °C during 48 h and ground for chemical analysis (see Table 1). We determined total carbon (C) as 50% of ash-free biomass (Schlesinger, 1977; McClaugherty et al., 1985; Gallardo and Merino, 1993), while total nitrogen (N) (ÓNeill and Webb, 1970), lignin (L), cellulose and hemicellulose (Goering and Van Soest (1970) were measured with an Autoanalyser (RFA 300-Alpken, Wilsonville, OR, USA) at the Chemical Analyses Laboratory of INTA Bariloche. The litter was air-dried and thoroughly mixed to form one common pool with equal amount of each species.

Litter bags (24 × 21 cm; $n = 72$) were constructed with 0.3 mm nylon mesh on the bottom side, and 1 mm nylon mesh on the upper side. The thinner mesh prevents leaf-litter loss from the bottom side, whereas the coarser mesh allowed the access of micro and mesofauna through the top side of the bag. The litter-bags were filled with 6 ± 0.02 g of the common substrate pool. In order to estimate true dry mass before litter-bag burial we first calculated air-dried water content. We air-dried five sub-samples of the leaf-litter substrate and oven-dried them at 50 °C for 48 h. Water content value (%) was deducted from air-dry mass in all samples.

In December 2009 six litter-bags were places on the soil surface of each of the 12 forest fragments, in two locations: edge (within 2 m from the end of the tree line) and interior (about 30 m from the end of the tree line). Each litter-bag was positioned with the thin mesh side in contact with soil, and the wide mesh side was covered with some of the natural litter layer of each fragment to simulate natural decomposition conditions. We retrieved all litter-bags after 120 days of incubation and immediately transported them in paper bags to the laboratory, where they were stored at −4 °C until processing. Samples were then defrosted, cleaned by removing soil material, and oven-dried at 60 °C for 48 h for dry mass determination. To correct for soil contamination, the remaining ash free dry mass (AFDM) for each litter-bag was measured by incineration at 550 °C for 4 h (Harmon and Lajtha, 1999). Decomposition rate was estimated as the difference between initial litter dry weight and litter dry weight after incubation, without ash.

2.3. Data analysis

To evaluate the effects of habitat fragmentation on leaf-litter decomposition we developed a linear mixed model (Pinheiro and Bates, 2000) with decomposition rate (% dry weight mass loss) as response variable. Fragment size (ha) and location (edge/interior) were treated as fixed effects. Site (fragment identity) was included
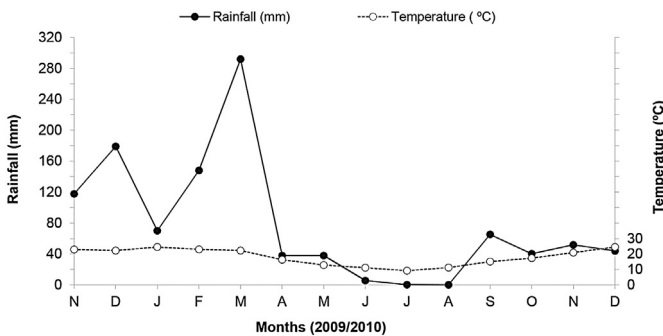

Fig. 1. Climodiagrams representing mean monthly temperatures and precipitation for the study site, taken from closest meteorological station (6 km from the fragments, Servicio Meteorológico Nacional Argentino) during the period of the experiment.

Table 1
Initial litter quality of two common plant species from Chaco Serrano forest.

	Nitrogen (%)	Carbon (%)	Lignin (%)	Cellulose (%)	Hemicellulose (%)
Celtis ehrenbergiana (Klotzsch)	1.76	71.40	5.1	14.9	0.1
Croton lachnostachyus (Baill)	1.49	42.36	6.3	23.7	1.6

as random factor to account for the non-independence of edge and interior in the same fragment. Location (interior/edge) was also incorporated as nested factor within site to contemplate the co-dependence of the three litter-bags from each location. We also evaluated interactions between fixed effects. Non-significant interactions were removed in order to obtain the most parsimonious model. Statistical analyses were performed using R 2.11.0 software (R Development Core Team, 2010). After checking data distribution, values were arcsine (percentage dry mass loss) or log (fragment size) transformed in order to achieve normal distribution.

3. Results

After 120 days of incubation (December 2009—April 2010) in the wet and warm season of Chaco Serrano (see Fig. 1), the decomposition of the common substrate varied between 50 and 85% mass loss (mean = 72.80 ± 1.41%). As forest fragment size decreased, decomposition rates also declined (Table 2, Fig. 2). Decomposition rates did not differ between the forest edge and the interior (Table 2). The effects of forest area and edge/interior location on decomposition rates were independent from each other since the interaction between these factors was not significant ($F = 0.46$; $p = 0.51$).

4. Discussion

In one of the first studies of leaf-litter decomposition simultaneously testing area and edge effects in a fragmented subtropical dry forest, we have shown decomposition rates of a common substrate declining with forest fragment size but no effect, or interaction, of location within fragment. Changes in fragment area could affect environmental conditions for decomposition via edge effects: as fragments become smaller, conditions in the interior approach those in the drier and hotter edge habitats. In such a scenario, decomposition should be expected to decrease at the edges and in smaller remnants, with integration between edge and interior in the latter, where edge conditions become prevalent. However, after 120 days of incubation, these hypotheses were not supported by our results, since decomposition rates did not differ between forest edge and interior habitats, nor did edge interact with forest area. Conversely, Hastwell and Morris (2013) found no effect of area on leaf-litter decomposition in an Australian forest, whereas decomposition rates decreased near edges depending on edge orientation.

Another possible mechanism for slower decomposition rates in smaller fragments could be related to species loss, affecting either
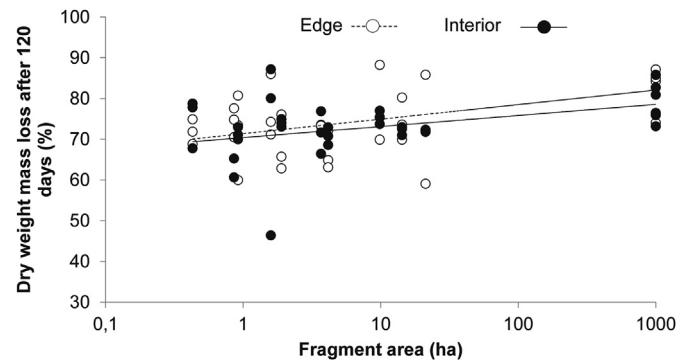

Fig. 2. Leaf-litter dry weight mass loss (%) after 120 days of incubation at edge and interior locations in forest remnants of Chaco Serrano.

litter quality (via changes in plant species abundance and identity, Noble, 2013) or the decomposer biota (Rantalainen et al., 2005). In our experiment, litter quality was kept constant by using the same substrate in all fragments, so it is not a change in litter quality that is causing slower decomposition in smaller fragments (Didham, 1998). Instead, *in situ* conditions and particularly the role of the decomposer biota in decomposition remain to be investigated. A reduction in fragment area has been linked to impoverished detritivorous fauna in rainforest systems (leaf litter beetles: Didham et al., 1998; termites: Davies, 2002; leaf-litter ants: Carvalho and Vasconcelos, 1999), with exclusion of soil invertebrates resulting in decreased leaf litter decomposition (Bradford et al., 2002; Meyer et al., 2011; Powers et al., 2009). A recent study found that slow decomposition of common substrates in forest patches was linked to changes in macroinvertebrate communities (Cuke, 2012).

In our study we did not detect any edge effects on litter decomposition. Edge effects on leaf-litter decomposition appear to be highly variable in different systems. For example, in tropical systems decomposition was either highest at forest edges or did not differ with position (Didham, 1998; Rubinstein and Vasconcelos, 2005). The opposite pattern was found in temperate forest (Riutta et al., 2012). Cardinal orientation of edges may also influence decomposition rates of litter (Romero-Torres and Varela Ramírez, 2011; Hastwell and Morris, 2013). Such variability could be related to the complexity of interactions between microenvironment and some characteristics of edge habitat. For example, increased temperature in forest edges may either enhance or slow decomposition depending on moisture content, which may in turn be modulated by edge orientation, altitudinal variations, type of matrix, among other factors (e.g. Gehlhausen et al., 2000; Romero-Torres and Varela Ramírez, 2011). To make the picture more complex, most studies on microclimatic changes between edge and interior habitats have focused on tropical systems (Laurance, 2004), whereas recent evidence has shown fragment interior being warmer and drier than edges in forests with discontinuous canopy cover, such as in Chaco Serrano (Wright et al., 2010). Finally, detection of edge-related changes depends on the distance used to define edge and interior habitats. In some systems, edge microclimatic changes can penetrate more than 40 m into the interior of a forest (Kapos, 1989; Davies-Colley et al., 2000). The distance between edge and interior samples in our study (30 m) might be deemed insufficient to perceive edge effects on leaf litter decomposition related to microclimate. Nonetheless, a similar design allowed detection of edge-related differences in herbivory and parasitism rates in forest remnants in Chaco Serrano (Valladares et al., 2006).

Table 2
Details of linear mixed models examining the relationship between edge/interior localization, fragment area (log) and dry weight mass loss (arcsine %) after 120 days of incubation in remnants of Chaco Serrano. Location (edge/interior) and fragment area were modelled as fixed effects whereas site (fragment identity) and location (interior/edge) nested within site, as random effects. SE (standard error), DF (degrees of freedom).

Term	Estimates ± SE	DF	F	p	StDev	Residuals
Intercept	1.01 ± 0.01	1, 48	12876.32	<0.0001		
Location (Edge/Interior)	-0.02 ± 0.02	1, 11	1.48	0.24		
Fragment area	0.04 ± 0.008	1, 10	18.09	**0.002**		
Random effects						
Site identity					2.86E-06	
Site identity (Location)					4.18E-07	0.07

Our study contributes to the scarce knowledge about habitat fragmentation effects on the decomposition process, providing evidence of negative effects of declining fragment size on leaf-litter decomposition. Further studies incorporating microclimate data, information about soil and litter moisture, as well as about structure and activity of soil biota are necessary in order to disentangle the potential mechanisms underlying such effects. Finally, more studies on patterns of decomposition from different ecosystems to unravel the role of the various controls of litter decomposition are needed in order to understand and predict decomposition and nutrient cycling patterns in fragmented landscapes.

Acknowledgements

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