Do leaf-cutting ants benefit from forest fragmentation? Insights from community and species-specific responses in a fragmented dry forest

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Abstract. 1. The expansion of agriculture has led to forest loss and fragmentation, resulting in dramatic biodiversity impoverishment. Surprisingly, few studies have assessed forest fragmentation effects on leaf-cutting ant assemblages, and none has dealt with effects on their community richness and composition, despite their known role as key herbivores and ecosystem engineers.

2. We analysed forest area and edge effects on leaf-cutting ant abundance, richness and assemblage composition, by recording and identifying colonies along edge and interior transects in 12 Chaco Serrano forest remnants of different sizes, in Central Argentina. We also explored leaf-cutting ant presence in the adjacent soybean matrix.

3. We recorded five leaf-cutting ant species, in the genus *Acromyrmex*. In the soybean matrix, colonies of three species were observed, which were also found at the forest edge. Within the forest, edges sustained more species and colonies than interior habitats, whereas forest area was linked positively to colony abundance. Taxonomic composition of leaf-cutting ant assemblages reflected both area and edge effects.

4. Our results revealed overall positive edge and area effects on leaf-cutting ant communities, highlighting differential species-specific responses and a possible role for *Acromyrmex crassispinus* as a forest status indicator. According to our findings, an increase in edge habitats may favour most leaf-cutting ant species, providing a suitable interface for access to the cultivated matrix, but hindering species associated with undisturbed forest conditions. As leaf-cutting ants are acknowledged as cornerstones of ecosystem functioning, the consequences of these trends may be far reaching.

Key words. *Acromyrmex*, area effect, dry forest, edge effect, habitat fragmentation.

Introduction

The expansion of agriculture has transformed original landscapes into a mosaic of crop and non-crop habitats (Vitousek *et al.*, 1997). Habitat fragmentation, or the subdivision of a once extensive habitat into a number of smaller and isolated remnants surrounded by a usually inhospitable matrix (Fahrig, 2003), is a major driver of the current global environmental change threatening Earth's ecosystems (Tylianakis *et al.*, 2008). Among the most affected systems, neotropical dry forests represent a top conservation priority, having lost more cover to

agriculture in comparison to other terrestrial biomes (Grau *et al.*, 2008).

Forest loss through fragmentation is largely responsible for dramatic losses of biodiversity (Fahrig, 2003; Ribas *et al.*, 2005). Smaller fragments usually sustain fewer species and smaller populations in comparison with large ones, a pattern consistent with the species-area relationship (Drakare *et al.*, 2006; He & Hubbell, 2011). Moreover, as remnants become smaller there is an increase in edge habitat, with various physical and biological changes at the intersection of the original system with the matrix (Laurance, 2008). Edge effects usually involve altered microclimatic conditions and result in complex ecological responses (Laurance *et al.*, 2002; Ries *et al.*, 2004; Ewers *et al.*, 2013) that may interact with area effects, although this interaction is seldom considered (Didham *et al.*, 2012). Also, because not all species are equally vulnerable to the effects of forest fragmentation (Cagnolo *et al.*, 2009), biological communities may be altered in their composition, beyond changes in species numbers.

Leaf-cutting ants (LCA) in the genera *Atta* and *Acromyrmex* (Hymenoptera: Formicidae) represent conspicuous key herbivores in the Neotropics (Fowler *et al.*, 1989; Urbas *et al.*, 2007), cutting fresh leaves and transporting them to their nest, to be used as substrate for fungal cultivars on which the ants actually feed (Hölldobler & Wilson, 1990). Leaf-cutting ants are considered 'ecosystem engineers' because their activities determine changes of the physical environment, leading to altered resource availability for other organisms (Farji-Brener *et al.*, 2010; Meyer *et al.*, 2013). They also have an important role in energy transfer, contributing to soil nutrient enrichment (Moutinho *et al.*, 2003) with effects spreading for tens of meters around the nests (Corrêa *et al.*, 2010). On the other hand, LCA can attain pest status on cultivated systems (Della Lucía, 2003), cutting up substantial amounts of the standing leaf crops (e.g. Zanetti *et al.*, 2003 but see Fowler *et al.*, 1989).

Surprisingly few studies have assessed forest area and edge effects on LCA abundance and, to our knowledge, none has dealt with effects on their community richness and composition. The available information shows increased LCA abundance at the artificially created edges (Wirth *et al.*, 2007; Meyer *et al.*, 2009; Dohm *et al.*, 2011) and in smaller forest fragments from which predators were excluded (Terborgh *et al.*, 2001), although another study found no differences in LCA nest densities (*Atta laevigata*) between fragments and continuous forest (Vasconcelos, 1988 in Vasconcelos & Bruna, 2012). Moreover, this information is based on tropical rainforests, with no reports from fragmented dry forests where microclimatic changes associated to edge effects may have a different impact.

Here, we analyse species richness, abundance and taxonomic composition of LCA assemblages in relation to forest remnant area and edge versus interior habitats, in a fragmented Chaco Serrano forest in central Argentina. This system, part of the most extensive and highly threa-tened dry forest in South America, lost 94% cover in just 30 years and is currently represented by isolated remnants within a predominantly agricultural matrix (Zak *et al.*, 2004). Fragmentation of Chaco Serrano forest has led to changes in plant and insect diversity and interactions (e.g. Valladares *et al.*, 2006; Cagnolo *et al.*, 2009; González *et al.*, 2014). Although there is no information on LCA in this system, despite them being acknowledged to be amongst the most important herbivores in the Chaco region (Bucher, 1987). To our knowledge, this is the first study simultaneously analysing area and edge effects on LCA assemblages. Moreover, considering the matrix role as a selective filter for species movement among forest fragments (Watling & Donnelly, 2006; Laurance *et al.*, 2007) and the notoriety of LCA as crop pests, we explored their presence in the agricultural matrix.

Given their frequent association with disturbed habitats, we expected richer LCA assemblages at the forest edges and in small fragments in comparison with those from core, large forest habitats. Moreover, differential responses due to varying degrees of vulnerability among species should lead to changes in assemblage composition driven by area and edge effects. Finally, we expected LCA not to construct their nests in the matrix or to restrict them to areas near to forest, given the seasonal resource instability linked to crop practices.

Materials and methods

Study area

The study was carried out in an area of Chaco Serrano in Central Argentina (31°09′S to 31°13′S and 64°13′W to 64°17′W), at 600–640 m.a.s.l., with 750 mm annual rainfall concentrated in the spring-summer months (October-April) and mean yearly temperatures ranging from 10 °C (minimum) to 26 °C (maximum). Native vegetation in Chaco Serrano, belonging to the most extensive dry forest in South America, is represented by a low and open woodland with a tree stratum up to 15 m high, 1–3 m high shrubs covering 10–80% of the ground, a herbaceous layer (up to 95% cover), and many vines and epiphytes (Cabido *et al.*, 1991).

Twelve forest remnants (including two continuous sites >1000 ha) were selected through digital satellite images and on-site observations. The remnants covered an area gradient from 0.42 ha to over 1000 ha and had been isolated (75–200 m from nearest remnant) for about 40 years, within a matrix currently dominated by wheat in winter and soy or maize in summer (Fig. 1).

In each remnant, active adult LCA colonies, i.e. with a soldier caste being present (Dohm *et al.*, 2011) were recorded along two 50 m long × 2 m wide belt transects at each of two locations: forest edge (within 5 m from the tree line) and forest interior (about 25 m from the tree line). All transects were parallel to the forest limit and distant at least 50 m from each other within each location.

Fig. 1. Aerial view of the study area, showing Chaco Serrano forest remnants included in the study (numbered).

This distance has been proved sufficient to detect edge effects in other studies within the same system (e.g. Valladares *et al.*, 2006; González *et al.*, 2014; Rossetti *et al.*, 2014). Samples of minor and major workers were taken for species identification. Sampling took place by running new transects in each fragment in two consecutive summer seasons (February–March 2010, 2011), and cumulative data were used for statistical analyses. In the matrix (soybean crop) adjacent to three large remnants, a similar sampling was carried out along two edge transects (5 m from the tree line) and two interior ones (25 m from the tree line), in March 2011.

Ant species were identified on the basis of morphological features of the collected individuals and nest features. We used published reference works (Santschi, 1925; Gonçalves, 1961; Kusnezov, 1978; Forti *et al.*, 2006), online references (AntWeb) and comparisons with specimens at the Museum of Natural Sciences Miguel Lillo (Tucumán, Argentina). Reference specimens have been deposited in the entomological collection of Cátedra de Entomología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba.

Data analysis

To detect possible effects of forest fragmentation on LCA communities, we analysed variations in colony abundance and species richness (pooled data from both years) as response variables in generalised linear mixed models (GLMMs), with a Poisson error distribution and a log link function. Fragment area (log transformed) and edge/interior location were included as explanatory variables, and site (fragment) as random effect, considering also the interaction between area and location. Similar models were used to search for effects on the abundance of each of the most common species. Analyses were performed using the software R (R Development Core

Team, 2014; version 3.1.1) and the function glmer in the package lme4 (Bates & Sarkar, 2007). Best models for each response variable were selected via backward elimination of non-significant explanatory variables using Likelihood Ratio Tests, starting from full models including variable interactions. When significant area × location interactions were detected, poisson regressions were performed to test separately for area effects on each location.

Variations in community taxonomic composition were also investigated by performing a principal component analysis (PCA), with standardised abundance data for all species. This analysis was performed with InfoStat (2010). Finally, to check the explanatory power of area and location on LCA assemblage composition, the first and second principal components were used as dependent variables in GLMMs models similar to those above described; residuals were normally distributed, therefore we used the Lme function from the nlme package (Pinheiro *et al.*, 2013).

Results

Leaf-cutting ant assemblages in the forest and the agricultural matrix

Five leaf-cutting ant species were recorded from 162 colonies in the studied remnants: *Acromyrmex (Acromyrmex) crassispinus* (Forel), *A. (Möellerius) heyeri* (Forel), *A. (Acromyrmex) lundi* (Guérin), *A. (Möellerius) silvestrii* (Emery), *A. (Möellerius) striatus* (Roger).

Leaf-cutting ants communities were dominated by *A. crassispinus* (41.6% of all colonies), *A. lundi* (21.32%) and *A. striatus* (16.75%). Only *A. crassispinus* and *A. lundi* were found in the forest interior, with a strong dominance of the first species. Instead, all five species were present at the forest edge, with *A. lundi* and *A. striatus* each accounting for a third of the colonies, followed closely by *A. crassispinus* (Fig. 2). Within the crop matrix (Fig. 2), LCA colonies were recorded only up to 5 m from the forest (none was found at 25 m from the forest) and included three species also found at the forest edge,
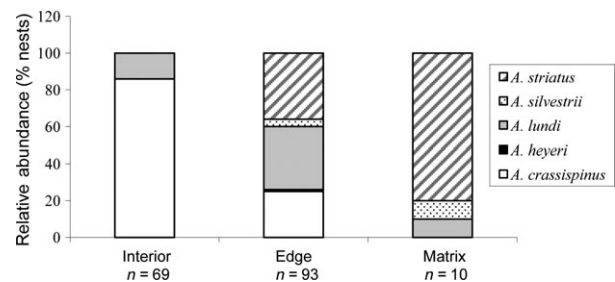

Fig. 2. Relative abundance of leaf-cutting ant species (% nests) recorded in fragmented Chaco Serrano forest interior, edge, and in the agricultural matrix.

of which *A. striatus* was strongly dominant. Only *A. lundi* was found in all three environments.

Forest area and edge effects on LCA species richness and abundance

Individual forest remnants yielded between one and four LCA species. Species richness was significantly higher at the forest edge, where it duplicated the value observed in the interior (Fig. 3a), but showed no relation to forest area (Table 1).

Between one and 29 LCA colonies were recorded along 800 m^2 of sampled transects in each forest remnant. The number of colonies showed a highly significant interaction between area and location, with fewer colonies being found in smaller forests, particularly at the interior (Fig. 3b; Table 1). Further separate regressions indicated that only colonies at the forest interior were significantly affected by area (interior: $P < 0.001$, deviance change = 46%; edge: $P = 0.253$, deviance change = 4%). Moreover, LCA tended to be more abundant (Table 1) at the edge (7.75 ± 1.22) than at the interior (5.75 ± 1.46).

When the dominant species were individually analysed, colony abundance of *A. crassispinus* (Fig. 4) was directly related to the size of the forest and noticeably higher at the interior (6.56 ± 1.57) than at the edge (2.56 ± 0.56) of each forest fragment, without interaction between area and location (Table 1). Variations in the number of colonies of *A. lundi* were independent of forest area and related to edge/interior location (Table 1), with three times more nests at the edge (3.56 ± 0.94) than at the forest interior (1.11 ± 0.39). Another abundant species, *A. striatus*, was solely found at the forest edges, where the

Table 1. Summary of results from Generalised linear mixed models evaluating effects of fragment area, interior/edge location and their interactions, on leaf-cutting ant communities (species richness and nest abundance), nest abundance of common species, and first and second components of PCA for community taxonomic composition, in Chaco Serrano forest. Only the explanatory variables retained in the models selected by Likelihood Ratio Tests are presented.

	Explanatory variables	X^2	P-values
LCA richness	*Edge/Interior*	6.91	0.009
LCA abundance	*Edge/Interior*	3.256	0.071
	Area	4.040	0.044
	Interaction	8.221	0.004
Acromyrmex crassispinus	*Edge/Interior*	16.356	<0.001
	Area	9.677	<0.002
Acromyrmex lundi	*Edge/Interior*	12.119	<0.001
1st PCA component	*Edge/Interior*	13.354	<0.001
2nd PCA component	*Area*	5.810	0.016

PCA, principal component analysis.

number of colonies (2.75 ± 2.53) was independent of area ($X^2 = 1.323$, $P = 0.253$).

Forest area and edge effects on LCA community composition

Taxonomic composition of LCA assemblages reflected both area and edge effects, according to results from PCA. The first PCA axis clearly separated assemblages found in the forest interior from those found in the edges (Table 1; Fig. 5). Forest size effects on these assemblages were instead
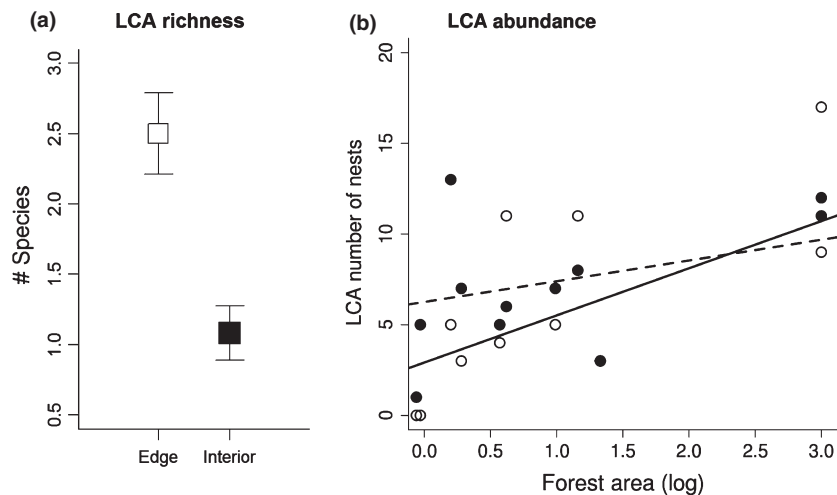

Fig. 3. (a) Species richness (mean and SD) and (b) abundance (number of colonies) of leaf-cutting ant assemblages at the edge and interior of Chaco Serrano forest remnants. The graphs depict significant results from Generalised Mixed Linear Models (see Table 1) from which lines in panel b were calculated (see Table 1 and Materials and methods section for more information). Black circles and solid line: forest interior, empty circles and dashed lines: forest edge. Some points are hidden due to data overlap.
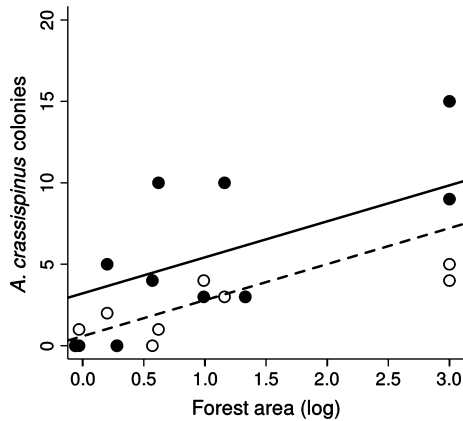
Fig. 4. Abundance (number of colonies) of *Acromyrmex crassispinus* in edge and interior habitats of 12 Chaco Serrano remnants of different sizes (ha). Lines were calculated from Generalised Mixed Linear Models. Black circles and solid line: forest interior, empty circles and dashed lines: forest edge. Some points are hidden due to data overlap.

revealed on the second axis (Table 1). The multivariate analysis also pointed out *A. crassispinus* as a typical interior species from larger remnants, whereas *A. lundi*, *A. silvestrii* and *A. striatus* were linked to edge locations (Fig. 5).

Discussion

The present work offers the first evidence of forest fragmentation effects on leaf-cutting ant communities in a subtropical dry forest, linking area and edge effects to changes in ant richness, colony abundance and taxonomic composition.

Leaf-cutting ant assemblages in the forest and the agricultural matrix

We recorded five LCA species, all within *Acromyrmex*, a genus particularly rich in subtropical and southern South America (Fowler & Claver, 1991). Leaf-cutting ant communities appear to be relatively rich in the Chaco Serrano forest, in comparison with only two (Sobrinho *et al.*, 2003; Wirth *et al.*, 2007; Lozano-Zambrano *et al.*, 2009; Meyer *et al.*, 2009; Leal *et al.*, 2012) or three species (Ribas *et al.*, 2005; Dohm *et al.*, 2011), mostly in the genus *Atta*, recorded from comparable studies carried out in fragmented tropical forests. This difference might be related to the greater diversity of the genus *Acromyrmex* in comparison with *Atta* (Fowler & Claver, 1991).

The forest edge, recruiting all five species, appeared to provide an adequate interface for species found in the forest interior as well as for those in the agricultural habitat. Instead, the cultivated matrix seemed inhospitable for *Acromyrmex* colonies beyond the forest proximity, where nests from three species were found. On the other hand, *A. striatus* accounted for two-thirds of colonies in the matrix despite it being absent in the forest interior, which suggests a specific association with disturbed habitats. This possibility is supported by the species pest status in some regions (Diehl-Fleig, 1993).
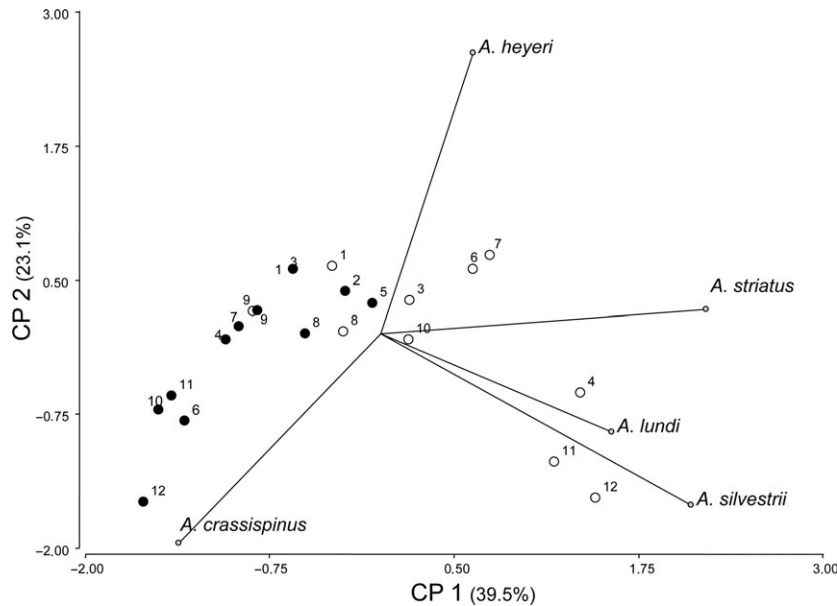

Fig. 5. Principal component analysis of leaf-cutting ant assemblages associated to edge and interior habitats of Chaco Serrano forest remnants of different sizes. Black circles: forest interior, empty circles: forest edge. Numbers next to each marker indicate forest size (increasing value = larger area, from 1 to 12 within edge and interior).

Forest area and edge effects on LCA richness and abundance

Biodiversity loss is the best known consequence of habitat loss in fragmented systems (Watling & Donnelly, 2006), a trend that has also been reported for some general ant communities (Vasconcelos *et al.*, 2006), but had yet to be assessed for LCA. In our study, LCA richness did not change with fragment area, as observed in fungus cultivating ants (Lozano-Zambrano *et al.*, 2009). As generalists tend to be less vulnerable to habitat loss (e.g. Cagnolo *et al.*, 2009), the wide plant range used by LCA species, as well as their preference for pioneer plant species (Farji-Brener, 2001) which are frequent in smaller fragments (Lozano-Zambrano *et al.*, 2009), may contribute to weaken the expected area effects on species richness. Nonetheless, forest area influenced LCA overall abundance interacting with edge effects, so that fewer LCA nests were found in smaller fragments, albeit only at the forest interior. Although positive area effects have been also observed on abundance of other ant communities (Carvalho & Vasconcelos, 1999; Schroeder *et al.*, 2004), the only previous information on LCA colonies showed them to be more abundant in smaller fragments, which was attributed to the absence of predators (Rao, 2000; Terborgh *et al.*, 2001).

We found nearly twice the number of species and colonies at the forest edge in comparison with the interior, thus supporting the view that leaf-cutting ant populations benefit from edge conditions (Wirth *et al.*, 2007; Dohm *et al.*, 2011). In addition, our results show that LCA edge-related proliferation, previously known only for *Atta* species in tropical forests, is indeed a widespread phenomenon as proposed by Dohm *et al.* (2011), affecting also *Acromyrmex* species in subtropical dry forests. Edge effects are particularly relevant because of the large extent and rapid expansion of edge habitats at the expense of core forest area, which may lead to over half of the remaining forests actually representing edge-forests (Broadbent *et al.*, 2008), on which the impact of LCA might be exacerbated (e.g. Urbas *et al.*, 2007).

Species responses to forest area and edge effects

The dominant *A. crassispinus* stood out by being the only species showing a strong positive relationship with fragment area and with the forest interior. Apparently thriving in the less disturbed situations within the forest and particularly vulnerable to fragmentation in the studied system, *A. crassispinus* might provide a valuable indicator of the forest status. The value of this species as an environmental indicator is enhanced by its characteristic large aboveground nests (Forti *et al.*, 2006) being easily censused. The remaining species presented a common pattern of higher abundance at the forest edges, in agreement with the generalised trend for LCA (Urbas *et al.*, 2007;

Wirth *et al.*, 2007; Meyer *et al.*, 2009; Dohm *et al.*, 2011). On the other hand, their lack of response to forest size suggests that the area effects observed at community level were driven by *A. crassispinus*. For most LCA species, possible negative effects of habitat loss might be compensated by enhanced favourable conditions because edge habitats increase in smaller remnants (Jaffe & Vilela, 1989; Urbas *et al.*, 2007). Variations in the degree of foraging specialisation or environmental requirements may drive species-specific trends. For example, different nesting habits linked to temperature variations across the soil profile. Thus, among the LCA species in our study, only *A. crassispinus* is known to build superficial nests both in shaded and exposed environments, whereas the remaining species have been linked to subterranean nests in exposed, warmer locations (Bollazzi *et al.*, 2008), in coincidence with our observations.

The differential responses to habitat fragmentation here described were reflected in changes in the taxonomic composition of LCA assemblages, which related mainly to edge/interior location with a lesser influence of forest size, thus supporting edge effects as the major organising factor for community structure (Ries *et al.*, 2004). It must be noted that some influence of pre-existing differences in ant communities on the observed patterns cannot be ruled out, due to lack of pre-fragmentation data and the non-random nature of the fragmentation process.

Summing up, our study provides novel information on LCA assemblages from a fragmented dry forest, showing greater overall abundance and richness at the forest edge and in larger forest fragments, with differential species-specific responses leading to changes in community composition, and suggesting a possible role for *A. crassispinus* as forest status indicator. Our results suggest that in the highly threatened South American dry forests (Grau *et al.*, 2008; Aide *et al.*, 2013), the escalating pervasiveness of edge habitats (Broadbent *et al.*, 2008; Wirth *et al.*, 2008) may favour most LCA species and provide an interface for access to the cultivated matrix, while hindering vulnerable species associated to undisturbed forest conditions. Given the importance of LCA as cornerstones of ecosystem functioning (Corrêa *et al.*, 2010), these trends and their possible consequences deserve further studies.

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