Herbivory, foliar survival and shoot growth in fragmented populations of *Aristotelia chilensis*

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ABSTRACT

Habitat fragmentation may modify ecological interactions such as herbivory, and these changes can impinge upon plant fitness. Through a natural experiment, we evaluated if herbivory, foliar survival and shoot growth of the evergreen tree *Aristotelia chilensis* differ between a continuous forest (600 ha) and small fragments ($\sim$3 ha) of the Maulino forest. From September 2002, we monthly recorded leaf emergence, area lost to herbivores and survival in four cohorts of leaves. Although herbivory of *A. chilensis* was low overall (foliar area loss <12%), herbivory was higher in the continuous forest than in small fragments. Nevertheless, differences in herbivory hold only for the first cohort of leaves, which were the largest ones. At the end of the growing season, herbivory rates in the continuous forest and fragments converge for all cohorts. Except for the first cohort of leaves, whose survival was higher in the fragments than in the continuous forest, foliar survival and shoot growth was similar in the continuous forest and fragments, and there was no correlation between herbivory and foliar survival or shoot growth. Although Maulino forest fragmentation negatively affects the intensity of herbivory, this effect is only transient, affecting only leaves that emerge early in the season, and might not affect the vegetative fitness of *A. chilensis* adults. The consequences of changes in ecological interactions triggered by forest fragmentation ought to be assessed rather than inferred from variations in patterns of resource use.

1.   Introduction

Deforestation and forest fragmentation are regarded as a worldwide menace to compositional, structural and functional biodiversity, disrupting ecological interactions and processes, with far reaching consequences upon biodiversity (Chapin et al., 2000; Laurance, 2002). Herbivory is one of those interactions. The transformation of a large continuous forest into a number of smaller and isolated patches might change the composition, abundance, and distribution of herbivorous insects, and therefore alter herbivory rates (Didham et al., 1996, 1998; Kruess and Tscharntke, 1994).

Variations in herbivory can shift recruitment dynamics of forests acting at different hierarchical levels. First, at the individual level, changes in herbivory can modify vegetative growth, survival and plant reproductive success (Marquis, 1984; Crawley, 1985; Hochwender et al., 2003). At the population level, changes in fitness such as a reduction in seed

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output, might alter recruitment dynamics, thus modifying seedling abundance and composition (Marquis, 1984). Finally, at the ecosystem level, changes in herbivory can alter nutrient dynamics, modifying the decomposition rate of damaged leaves, hence nutrient availability for future recruits (Belovsky and Slade, 2000; Chapman et al., 2003).

Due to the modular nature of plants, herbivory can affect the population dynamic of leaves impinging upon plant photosynthetic rate and consequently on shoot growth (Bazzaz and Harper, 1977). Herbivores may affect leaf performance by reducing the leaf area available to capture energy, by removing nutrients and increasing the likelihood of pathogenic disease or death (Dirzo, 1984, 1987; Pritchard and James, 1984). Herbivory then, might affect leaf survival, and thus leaf demography. Consequently, the analysis of leaf demography is an appropriate methodology to elucidate the fate of the whole plant (Bazzaz and Harper, 1977; Abul-Faith and Bazzaz, 1980; Dirzo, 1984).

Although the potential impacts of herbivory on plant performance has been largely recognized, herbivory and plant performance variations with forest fragmentation have been rarely studied. The few studies so far published pinpoint that the frequency of damaged leaves or the amount of foliar surface lost to herbivores decreases in small forest fragments compared to continuous forests (e.g., Bresciano et al., 1999; Benítez-Malvido, 2001; Arnold and Asquith, 2002). However, increased herbivory could also be the outcomes of forest fragmentation (Lienert et al., 2002a,b). Regardless of such outcome, usually, the consequences of changes in the magnitude of herbivory are inferred rather than assessed. Despite the tight relationship between herbivory and plant fitness, whether changes in foliar surface lost to herbivores translate into altered foliar survival rates or shoot growth is yet to be assessed.

The Maulino forest of central Chile, a unique temperate ecosystem, has been intensively deforested and fragmented, initially due to increased fuel wood production and cultivation, and more recently, due to its replacement by *Pinus radiata* D. Don (Pinaceae) plantations (Lara et al., 1996; San Martín and Donoso, 1996). Currently, this forest remains as many small scattered fragments embedded in a matrix dominated by *P. radiata* (San Martín and Donoso, 1996; Bustamante and Castor, 1998; Grez et al., 1998). Forest fragments hold different herbivorous insect assemblages and exhibit altered plant–animal interactions such as reduced pollination and increased granivory rates compared to the continuous forest (Donoso et al., 2004; Jaña and Grez, 2004; Valdivia et al., 2006). We aim to assess the effects of the Maulino forest fragmentation on the herbivory and its potential impact upon foliar survival and shoot growth of adults of *Aristotelia chilensis* (Mol.) Stuntz (Elaeocarpaceae).

2. Methods

2.1. Study site

The Maulino forest is distributed between 35° 55′ S and 37° 20′ S, ranging from 100 to 900 m a.s.l. This forest harbors a group of endemic tree species, including *Gomortega keule* (Mol.) Baillon, the single species representative of the primitive family Gomortegaceae. The dominant species is *Nothofagus glauca*

(Phil.) Krasser (Fagaceae), which coexists with many endangered endemic species such as *Nothofagus alessandrii* Esp. (Fagaceae), *Pitavia punctata* (R. et P.) Mol. (Rutaceae), and *G. keule*.

2.2. Study species

Aristotelia chilensis is an evergreen native tree species, distributed in central Chile between 31° S and 40° S. The production of new leaves and shoot growth occurs largely in spring. Previous experimental evidence has shown that defoliation of *A. chilensis* trees does depress plant growth (Damascos and Prado, 2001a). In the Maulino forest, *A. chilensis* is distributed both in the continuous forests and forest remnants, being a common understorey tree. It is regarded as an early successional species (Hoffman, 1997) and usually these species have a higher degree of herbivory compared to later successional ones (Cates and Orians, 1975). These attributes render *A. chilensis* an adequate model to test the effects of forest fragmentation on herbivory.

2.3. Study design

The study was conducted during the spring–summer 2002–2003, a time span when new leaves of *A. chilensis* expand and when the highest abundances of herbivorous insects are reached in the Maulino forest (Jaña and Grez, 2004). To evaluate the effect of fragmentation on herbivory, foliar survival and shoot growth of *A. chilensis*, we compared them among individual plants growing at a continuous forest, within which is the Los Queules National Reserve, and surrounding fragments. The Reserve is one of only two areas allocated to preserve the Maulino forest. It covers 147 ha but it is part of a larger tract of continuous, privately owned forest, making up a single area of at least 600 ha, one of the largest extant tracts of Maulino forest. For our purposes, this large forest remnant is defined as "continuous forest". This study was also conducted in three small fragments adjacent to the continuous forest. These fragments were 3.4, 3.0, and 2.3 ha, separated from each other by at least 1 km. Both the continuous forest and fragments were surrounded by 20 year old *P. radiata* plantations. Fragments are, therefore, 20+ years old (see Donoso et al., 2004 for a map of the area).

In September 2002 (early spring), we marked 15 trees of similar size and appearance at the continuous forest and five at each one of three forest fragments. Spacing of sampled trees in fragments ranged from 3.5 to 3000 m and in the continuous forest from 4.0 to 600 m. In each tree, we randomly selected two branches exhibiting initial emergence of leaves. Each leaf was individually labeled with a plastic tag. Monthly, from September to December 2002, we identified and marked individually all newly emerged leaves per branch. This allowed us to evaluate monthly (until March 2003, early autumn) the herbivory and foliar survival of four cohorts of leaves: first cohort, those leaves that emerged during September; second cohort, those leaves that emerged during October; third cohort, leaves that emerged during November, and fourth cohort, those leaves that emerged during December 2002. After December, few if any leaves emerged (Fig. 1). This time span is biologically meaningful, because in *A. chilensis* the largest proportion on leaves are produced in early spring and senesce in autumn. A few leaves are produced in

summer, and though they may survive winter and senesce as late as the next spring, they are a minor proportion of all leaves (Damascos and Prado, 2001b). Therefore, we covered most of the life cycle of leaves of *A. chilensis* that emerged in spring. Furthermore, in central Chile and particularly at the Maulino forest, herbivorous insects are significantly more abundant in spring and summer (Fuentes et al., 1981; Jaña and Grez, 2004). Most defoliating activity then, is concentrated in these two seasons. Finally, the higher proportion of photosynthetic activity relevant for present and future plant requirements occurs during this period (Mooney and Ehleringer, 1998), thus the consequences of herbivory should be more important then.

Following the fate of the individually labeled leaves of four cohorts prevented underestimation of herbivory due to complete consumption of leaves (Lowman, 1997). We considered a leaf to be dead when it turned from green to brown (dead tissue) or when it was detached from the stem.

2.4. Herbivory

After Dirzo and Domínguez (1995), we assessed herbivory as the percentage of leaf area loss, using the following categories (C): 0, no area loss; 1, 1–6%; 2, 6–12%; 3, 12–25%; 4, 25–50%; 5, 50–100%. This score was used to define an index of herbivory (IH): $IH = (\Sigma n C_{0-5})/N$, where n is the number of leaves from a C category which goes from 0 to 5 and N is the total number of leaves studied in the two branches (Dirzo and Domínguez, 1995). This method renders herbivory values as accurate as other quantitative methods such as image processing (Rodríguez-Auad and Simonetti, 2001). In order to ensure consistency, measurements were always done by the same person (P.A.V.).

By March 2003, we calculated a cumulative herbivory index per tree, considering the herbivory upon all leaves (i.e., belonging to different cohorts, estimated with the same formula used above) weighted by the number of leaves of each cohort surviving at that time.

2.5. Foliar survival and shoot growth

We followed all surviving leaves in the two branches of a tree each month, from the emergence time until March 2003. Foliar
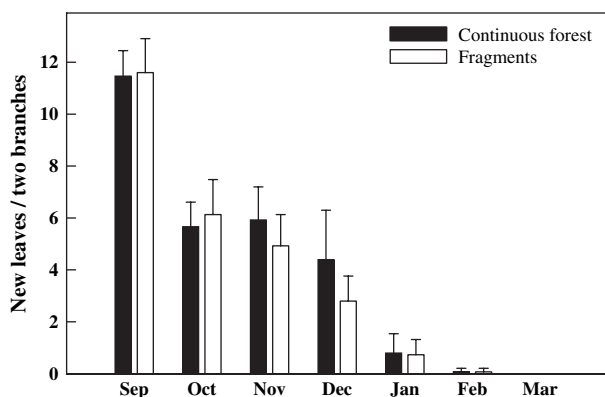
Fig. 1 – Production of new leaves in the continuous forest and fragments. Figures are the mean ± SE of the number of leaves emerging at two branches per tree. N = 15 trees in the continuous forest and 15 trees in forest fragments.

survival of each cohort was estimated through $lx = Nx/N_0$, lx is the proportion of leaves that survived to March, N_0 is the initial number of leaves, and Nx is the number of leaves that survived at March (Damascos and Prado, 2001b). Similar to herbivory, at the end of the study we calculated the cumulative foliar survival per tree, by adding the number of leaves from all cohorts still alive at this time of the year. We further assessed shoot growth as G: $(L_t - L_i/L_i)$ where L_t is the shoot length at the end of the growing season and L_i is the length at September 2002.

2.6. Data analysis

For leaf production and herbivory we pooled the data from the two branches of each tree as a single sample. For the analysis of shoot growth, we averaged the final length of the two branches of each tree and used the average as a replicate.

Difference in herbivory between trees within the continuous forest and fragments was spatially independent. That is, herbivory values were unrelated to distance between trees (Mantel test, 10,000 iterations, $r_s < 0.05$, $P > 0.30$ (one-tailed test) in all cases). Therefore, each tree was considered a replicate. For all cohorts, herbivory was similar between fragments (rmANOVA for the difference between fragments, Cohort 1: $F_{(2, 12)} = 0.24$, $P = 0.71$; Cohort 2: $F_{(2, 10)} = 3.25$, $P = 0.07$; Cohort 3: $F_{(2, 8)} = 0.05$, $P = 0.95$, and Cohort 4: $F_{(2, 6)} = 2.74$, $P = 0.10$). Therefore, we pooled the data from the three fragments. We also performed a power test to examine potential effects of sample size on statistical analysis, using nQuery advisor 6.0.

The effects of habitat fragmentation on leaf production and herbivory were examined using repeated measures one-way ANOVAs. For each cohort, the effect of habitat fragmentation on the foliar survival was analyzed using logistic regression analysis. Differences in shoot growth were assessed with a one-way ANOVA. Spearman rank correlations were used to assess associations between herbivory and leaf survival, as well as herbivory and shoot growth. All the statistical analyses were run in Statistica 6.0.

3. Results

Overall, we registered approximately 800 leaves, produced largely from September to December. From the beginning and throughout the growing season, the production of new leaves of all cohorts was similar in both the continuous forest and fragments (repeated measures ANOVA, $F_{(1, 28)} = 0.55$, $P = 0.47$; Fig. 1). On average (±standard error), 27.1 ± 1.9 leaves/two branches (pooling all cohorts) flushed between September and December in the continuous forest and 25.5 ± 1.8 in the forest fragments.

Herbivory was low both in the continuous forest and in the fragments, with an index of damage <2 (i.e., less than 12% of the foliar area removed; Fig. 2). Herbivory was higher in the continuous forest than in fragments. However, this difference was statistically significant only for the first cohort of leaves (Table 1). For the fourth cohort, there was also a significant interaction between time and fragmentation, with a higher herbivory in the continuous forest at the beginning of the emergence of leaves (Fig. 2, Table 1). For this cohort, herbivory
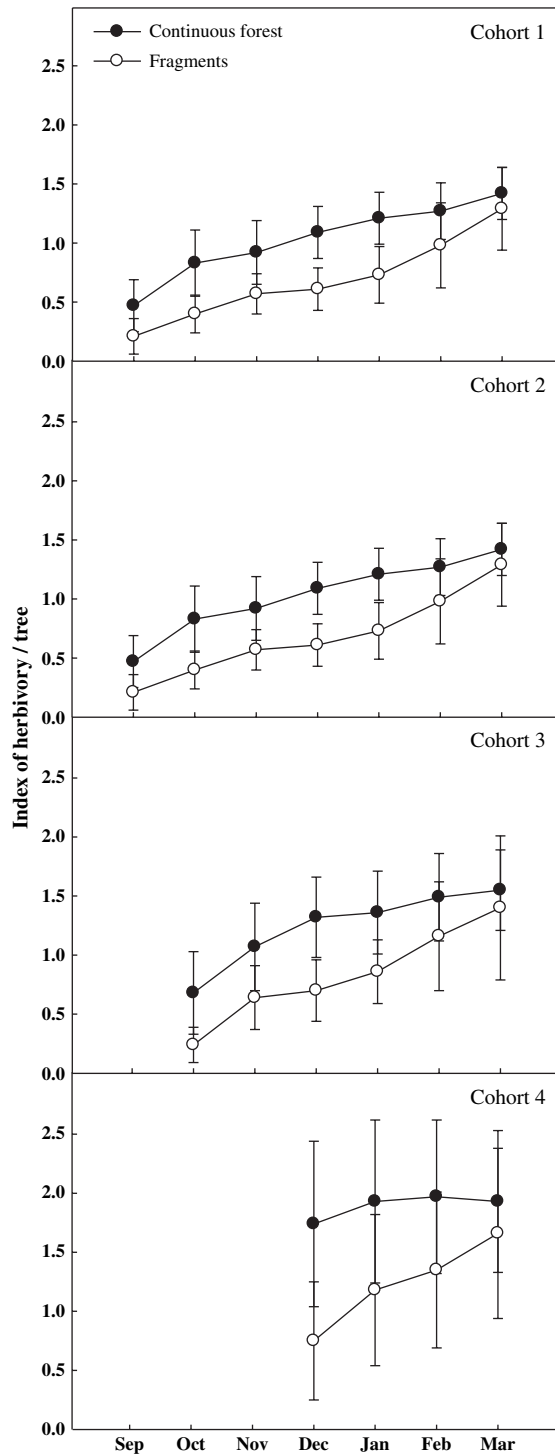
Fig. 2 – Herbivory of *A. chilensis* in the continuous forest and fragments, for the four cohorts of leaves: Cohort 1 (September), Cohort 2 (October), Cohort 3 (November) and Cohort 4 (December). Index of herbivory: 0, no area loss; 1, 1–6%; 2, 6–12%; 3, 12–25%; 4, 25–50%; 5, 50–100%.

Table 1 – Results of a repeated measures ANOVA for the effects of forest fragmentation on the herbivory of different cohorts of *A. chilensis* leaves

Source	df	F	P
Cohort 1			
Fragmentation	1	5.57	0.02
Error	28		
Time	6	43.07	$P \ll 0.0001$
Fragmentation × time	6	1.57	0.16
Error	168		
Cohort 2			
Fragmentation	1	3.38	0.08
Error	28		
Time	5	23.44	$P \ll 0.0001$
Fragmentation × time	5	1.18	0.32
Error	140		
Cohort 3			
Fragmentation	1	1.29	0.26
Error	28		
Time	4	16.47	$P \ll 0.0001$
Fragmentation × time	4	0.58	0.68
Error	112		
Cohort 4			
Fragmentation	1	2.15	0.15
Error	28		
Time	3	8.38	$P \ll 0.0001$
Fragmentation × time	3	3.51	0.02
Error	72		

0.57 for cohort 1, 0.40 for cohort 2, 0.17 for cohort 3 and 0.31 for cohort 4 (average: 0.36). The power of the between-month analysis conducted among months for each cohort was 0.99 for cohort 1, 0.99 for cohort 2, 0.99 for cohort 3 and 0.93 for cohort 4 (average 0.98).

Foliar survival was high, with more than 80% of leaves of all cohorts in the continuous forest and the fragments surviving until March (Table 2). For the first cohort, foliar survival was statistically higher in fragments than in the continuous forest. In the other cohorts though, survival did not differ significantly between habitats (Table 2). After pooling all cohorts, foliar survival was unrelated to herbivory at both the continuous forest and the fragments ($r_s = 0.06$; $P = 0.83$; $r_s = 0.24$; $P = 0.39$ for continuous and fragmented forest, respectively).

Although shoot growth was 1.2 times higher in the continuous forest, it did not differ significantly between the continuous forest (1.8 ± 0.2) and forest fragments (1.4 ± 0.2; $F_{(1,\ 28)} = 1.89$, $P = 0.17$). Additionally, no statistically significant correlation

in the continuous forest was high from the beginning of leaf emergence compared to the herbivory sustained by newly emerged leaves in other cohorts (Fig. 2). At the end of the study, herbivory in the continuous forest and fragments became similar in all cohorts. The statistical power of the between-habitat analysis (continuous forest vs. fragments) was

Table 2 – Results of the logistic regression analyses for the effect of habitat fragmentation on the proportion of *A. chilensis* leaves surviving until March (initial number of leaves are indicated in brackets)

Cohort	Continuous forest	Fragments	df	Wald	P
1	81 (172)	89 (174)	1	5.23	0.02
2	96 (85)	96 (92)	1	0.08	0.78
3	92 (89)	88 (75)	1	0.78	0.38
4	82 (66)	93 (42)	1	2.44	0.12

was detected between herbivory and shoot growth at both the continuous forest and the fragments ($r_s = 0.30$; $P = 0.27$; $r_s = 0.31$; $P = 0.26$, for continuous and fragmented forest, respectively).

4. Discussion

Herbivory affects plant performance, and changes in herbivory rates brought about by forest fragmentation could translate into altered plant growth and survival. At the Maulino forest, herbivory upon *A. chilensis* decreases in forest fragments, a phenomenon depicted by seedlings of this and other tree species in this fragmented forest (J.A. Simonetti, unpublished data), and occurs with other plant species in fragmented tropical and temperate forests (Benítez-Malvido, 2001; Groom, 2001; Arnold and Asquith, 2002). Therefore, forest fragmentation seems to have a consistent depressing effect on herbivory (but see Lienert et al., 2002a,b).

Nevertheless, the difference in the intensity of herbivory in the continuous forest and fragments was transient. The loss of leaf area was higher in the continuous forest only for the first cohort of leaves (i.e., leaves emerging in September), and for the newly emerged leaves of the fourth cohort (December). Then, towards the autumn, herbivory for all cohorts became similar. The decline of the effects of fragmentation on herbivory through time also occurs in seedlings in tropical forests. In Manaos, herbivory was higher in the continuous forest only during the first year of seedlings' exposure to herbivores, but later, differences in herbivory vanished (Benítez-Malvido, 2001).

Lack of differences in herbivory in the second to fourth cohort need to be viewed cautiously due to our low statistical power for between-habitat analysis. In fact, herbivory values are consistently higher at continuous forest than at forest fragments across the four cohorts (Fig. 2), but differences are statistically significant only in cohort 1. We cannot discard that these differences become significant in all cohorts if sample sizes were larger. Ongoing experiments will help us to conduct stronger statistical tests and consequently to disentangle the causal relationships among leaf herbivory, herbivore numbers and plant performance.

At the Maulino forest, like in the Mediterranean shrublands of Central Chile, insects are the most important herbivores (Fuentes et al., 1981). Although precise mechanisms remain to be explored, the reduction in the intensity of herbivory in fragments might result from depressed populations of herbivorous insects (Jaña and Grez, 2004). In fact, during spring and summer, the season when *A. chilensis* leaves expand, herbivorous beetles and flies are less abundant in small remnants than in continuous forest (Jaña and Grez, 2004). Furthermore, insectivorous birds are more abundant and prey significantly more on insects in forest fragments than in continuous forest (González-Gómez et al., 2006) which may depress the feeding activity of insects, rendering a reduced amount of folivory. Differences in palatability between leaves produced in fragments vs. continuous forest can be ruled out as insects do not discriminate leaves from forest and fragments (J.A. Simonetti et al., unpublished data).

At the continuous forest, herbivory on the fourth cohort was very high when they emerged in December, compared to the forest fragments and other cohorts. At this time, herbivorous insects reach their highest abundance at the Maulino forest, particularly at the continuous forest (Jaña and Grez, 2004). Therefore, newly emerged and potentially more palatable leaves might have been preferred by insects compared to fully expanded, older leaves from other cohorts. Furthermore, the convergence in the herbivory in the continuous forest and fragments by autumn might also be a consequence of the fact that at the Maulino forest, herbivorous insects decrease abruptly during autumn, and are no longer more abundant at the continuous forest (Jaña and Grez, 2004). Therefore, changes in consumer abundance could account for altered herbivory in fragmented Maulino forest.

A depressed interaction rate is not the single outcome for plant–animal interactions at the fragmented Maulino forest though. Similar to herbivory, pollination is reduced in forest fragments, lowering reproductive output of plants like *Lapageria rosea* (Valdivia et al., 2006) but granivory is significantly increased in the same forest remnants. Consumption of tree seeds like *N. glauca* is 34% more intense in fragments due to the higher abundance of granivores such as rodents and birds in this habitat (Donoso et al., 2004). Therefore, fragmentation does not affect plant–animal interactions in the same direction, leading vegetation dynamics in directions significantly different than in the continuous forest (Bustamante et al., 2005).

At the Maulino forest, herbivory of adult *A. chilensis* was low, with less than 12% of the leaf area lost to herbivores during the growing season. This low level of herbivory is also a common phenomenon in other temperate and tropical forests (Lowman, 1997), and might not translate into changes in fitness-related attributes. While complete experimental defoliation of *A. chilensis* depresses shoot growth by 50% (Damascos and Prado, 2001a), leaf area lost to herbivores in the Maulino forest does not affect it. Either the level of herbivory might be low enough not to impinge upon resource allocation to growth or *A. chilensis* is capable of compensating for the removed tissues after herbivory (Crawley, 1998). Compensation is more likely when herbivory occurs early in the growing season, thus giving the plant enough time to use accumulated photosyntates (Crawley, 1998), as might be the case for *A. chilensis*.

Foliar survival was higher than 80% in all cohorts and habitats, and only for the first cohort was it lower in the continuous forest. This reduced survival could be accounted for by the higher herbivory in the continuous forest than in the fragments at this stage. At no other cohort there were significant differences either in leaf survival or in herbivory. Nevertheless, when all leaves are considered, leaf survival is unrelated to herbivory, suggesting that current herbivory levels are low enough to impinge upon it, similar to the lack of effects of herbivory upon shoot growth. Thus, despite a reduction in herbivory, plant performance, assessed by shoot growth and foliar survival, is not substantially different in fragmented forests, suggesting that a reduction in herbivory in forest fragments of the Maulino forest does not convey advantages for plants.

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