



The effect of spatial context and plant characteristics on fruit removal



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ABSTRACT

Attracting frugivores for fruit removal is a crucial step in the reproductive success of those plants that depend on animals for seed dispersal. This mutualism involves many plant extrinsic and intrinsic factors that affect fruit removal. Along the northern portion of the temperate forest of southern South America, the nocturnal marsupial *Dromiciops gliroides* is the only effective disperser of the mistletoe *Tristerix corymbosus*. This system, where a single disperser removes the fruits of a plant is simple compared to systems that include multiple dispersers and represents a unique opportunity to study the effect of extrinsic and intrinsic factors in frugivore plant choices for fruit removal. With a hierarchical model, we evaluated the effects of spatial context (accessibility and tree cover) and plant characteristics (age and crop size) in fruit removal during four fruiting seasons. While all these variables affected fruit removal, only accessibility and plant age had consistent and positive effects across years. After studying four fruiting seasons, we found that characteristics associated with frugivores' habits are the most important factors for the reproductive success of plants dispersed by animals.

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1. Introduction

Fruit removal is a key process in the reproductive success of those plants that depend on animals for seed dispersal (Schupp et al., 2010). The visit of a frugivore to a plant, and the subsequent fruit removal from it, involves many extrinsic and intrinsic factors (Cortes and Uriarte, 2013). On one hand, habitat structure and the spatial distribution of resources (i.e. food, refuge) affect animal movement and space use. This means that frugivores might visit plants based on habitat features and conditions in the vicinity of plants (Carlo et al., 2007; Fedriani, 2005; Morales and Carlo, 2006; Robledo-Arnuncio et al., 2014). On the other hand, fruit traits (such as size, shape and nutrient content) as well as crop size also affect the probability of fruit removal (Izhaki, 2002; Jordano, 2000). Therefore, the reproductive success of animal-dispersed plants will emerge from the interplay between plant traits, their spatial context and frugivore behaviour (Blendinger et al., 2008; Carlo and Morales, 2008; Prasad and Sukumar, 2010).

In this context, plants that are located in places with high local fruit production (Carlo and Morales, 2008; Morales et al., 2012; Saracco et al., 2005; Sargent, 1990), surrounded by shelters (Fedriani, 2005; Perea et al., 2011; Russo and Augspurger, 2004) or

near corridors (Levey et al., 2005) may have higher visitation rates than plants that are isolated in the landscape. Moreover, the spatial configuration and availability of perches or sleeping sites can modify fruit removal (González-Zamora et al., 2012; Heelemann et al., 2012; Sasal and Morales, 2013). Regarding intrinsic factors, fleshy-fruited plants evolved fruit traits to attract suitable dispersers. For instance, fruit size and organoleptic characteristics—e.g. tannin or fat content—may determine foraging preferences of dispersers (Morán-López et al., 2015; Wang and Yang, 2015) and in general, larger crop size is related to increased removal rates (Moegenburg and Levey, 2003; Ortiz-Pulido et al., 2007; Takahashi and Kamitani, 2004). Thus, many factors affect visit rates by frugivores simultaneously and it is difficult to disentangle their net effect. Nevertheless, studying extrinsic and intrinsic factors simultaneously may shed some light on the relative importance of these factors in frugivores foraging decisions, and hence, in plant reproductive success.

For aerial hemi-parasitic plants (mistletoes), fruit removal and seed dispersal represent key stages in their life cycle (Aukema, 2003; Mathiasen et al., 2008; Norton and Carpenter, 1998). Mistletoes depend on frugivores that ingest their fruits and transfer the seeds to suitable hosts. Most mistletoes are dispersed by birds, but *Tristerix corymbosus* (Loranthaceae), is the only known mistletoe species dispersed by a marsupial, *Dromiciops gliroides* (Microbiotheriidae) (Amico et al., 2011; Amico and Aizen, 2000; di Virgilio et al., 2014). *Dromiciops gliroides* is a small (body mass ~ 27 g)

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arboreal and nocturnal marsupial; it has a prehensile tail and an opposable thumb that allows it to move swiftly through the forest. *Dromiciops gliroides* is not merely the disperser of *T. corymbosus* but also a key seed disperser in the temperate forest of South America where half of the plant genera (about 85 species) produce fleshy fruits (Aizen and Ezcurra, 1998; Amico et al., 2011, 2009; Amico and Aizen, 2000). This system, where a single disperser removes the fruits of a plant is simple compared to systems that include multiple dispersers and represents a unique opportunity to study the effect of extrinsic and intrinsic factors in frugivore fruit removal.

Given the importance of this mutualism at ecosystem level, it has been subject of several studies. The abundance of *D. gliroides* at the landscape scale depends on the availability of nesting sites and food (Rodríguez-Cabal and Branch, 2011) and, in turn, local abundance of this disperser shapes the spatial configuration of mistletoe populations (García et al., 2009; Magrath et al., 2015). As fruit availability and disperser abundance can vary from year to year, it is important to study several years in order to draw conclusions about the effects that both extrinsic and intrinsic factors have on fruit removal. Here, we evaluated during four fruiting seasons: (i) the effect of two spatial context characteristics, accessibility and tree cover; and (ii) the effect of two plant characteristics, crop size, and age index. Accessibility and tree cover could be important factors for arboreal animals. Also, as *D. gliroides* moves through the forest on shrubs and trees branches, and is susceptible to predation by raptors, we expect accessibility to be an important factor in foraging decisions allowing a safe way to the plant. Likewise, plants with higher tree cover may pose lower predation risk than plants with lower tree cover. Among intrinsic factors, crop size is a well known variable affecting fruit removal rates, and plant age could be related to fruit quality and quantity. In the present study, we analyse four fruiting seasons, with the aim to disentangle the importance of spatial context and plant characteristics in fruit removal.

2. Methods

2.1. Study site

This study was conducted in Llao-Llao Municipal Park, at 25 km West from San Carlos de Bariloche, Río Negro, Argentina (41° 0' S, 71° 30' W). Mean annual precipitation is approximately 1800 mm, and mean temperatures are 15 °C in summer and 3 °C in winter. Vegetation of the Northern Patagonian temperate forest is composed of two distinct layers: a lower shrub layer and a higher tree layer. *Nothofagus dombeyi* (coihue) and *Austrocedrus chilensis* (austral cypress) dominate the tree layer, while the bamboo *Chusquea culeou* and small trees such as *Aristolelia chilensis* (maqui), *Maytenus boaria* (maitén) and *Azara microphylla* (chin-chin) grow in a diverse shrub layer.

Tristerix corymbosus (Loranthaceae) is a mistletoe distributed along the Pacific coast of South America (Kuijt, 1988), between 32° and 42° S. This mistletoe is the only native plant that blooms during winter, flowering from late March to November (Aizen, 2003). Reproductive plants produce hundreds of fruits gathered in corymbs. The fruits consist in green pseudo-berries, each containing one seed of about 0.6 cm long, surrounded by a viscous sweet pulp (Amico and Aizen, 2000). Fruit size does not vary widely within or among mistletoes in our study site (length (CV = 6%), diameter (CV = 5%); Amico, Unpublished results). The fruits ripe between December and May and after a few weeks, if not removed, they wither in the plant. This senescent fruits have a wrinkled pericarp and a black, bitter pulp (Aizen, 2003). This mistletoe is a very important food item for this marsupial and the most consumed fruiting plant at our study site (Amico et al., 2009; García et al.,

2009).

2.2. Selection of focal plants

During four fruiting seasons (2008/2009, 2009/2010, 2010/2011 and 2012/2013), we selected 18–21 plants, located at least 10 m apart from each other, all parasitizing *Aristolelia chilensis*. The selected plants were different every year and were located in a wide variety of spatial contexts (accessibility and tree cover) in an area of 4 ha (Table A1). During the 2011/2012 season, data collection was not performed for safety reasons due to the massive population outbreak of rodents, particularly *Oligoryzomys longicaudatus*, *Abrothrix longipilis* and *Abrothrix olivacea* (Muridae) associated with the *C. couleu* bloom (Holz and Palma, 2012).

Between mid-December and May, we visited the selected plants every 7–15 days. In each visit, we counted the total number of corymbs present on each plant and we randomly selected ten corymbs in order to count the total number of fruits and the number of ripe, senescent, and removed fruits. Fruits removed by *D. gliroides* are clearly recognized because it leaves the pedicel after removal (Aizen, 2003).

2.3. Spatial context and plant characteristics

To characterize the spatial context of each plant, we measured accessibility, tree cover and shrub cover. To characterize the plant we measured the length of the longest branch and crop size. As, shrub cover was positively correlated with tree cover (Pearson's 0.32, $p < 0.05$) we did not include it in further analyses. Accessibility was defined as the percentage of nearby branches to the focal plant through which individuals of *D. gliroides* could move without descending to the ground. In order to quantify accessibility we divided the space around the plant in 8 parts within a 1 m radius. A plant with 100% accessibility had connections through the eight sections, while a plant with 0% accessibility had none. We estimated tree cover visually as the percentage of canopy cover over the focal plant. In order to estimate plant age we measured the length of the longest branch (LLB). Rodríguez-Cabal et al. (2007) found that, among several plant characteristics, LLB is the best estimator of *T. corymbosus* age: $\text{age (in years)} = 0.086 * (\text{LLB in cm}) + 1.968$ ($n = 40$, $r^2 = 0.73$). However, LLB is not a good estimator of plant size because many plants have one long branch but small overall size or volume (Rodríguez-Cabal, 2003). Finally, for every plant we calculated a crop size index following Morales et al.

(2012): $\text{Crop size index}_i = \sum_{t=1}^T \left[\text{mean}(f_{i,t} + d_{i,t} + r_{i,t}) \right] \times \frac{K_{i,t}}{T}$. This crop size index is a better estimator of fruit abundance than the total number of fruits per plant, as it represents the average number of fruits available for removal at every sampling occasion at each plant. Where $f_{i,t}$ is number of ripe fruits at plant i at time t , $d_{i,t}$ are senescent fruits, $r_{i,t}$ are removed fruits $K_{i,t}$ is the total number of corymbs and T the total number times we visited the plants.

2.4. Fruit removal

To analyse the effect of spatial context and plant characteristics in fruit removal rate we built a hierarchical regression model with accessibility, tree cover, LLB and crop size index as explanatory variables. Before fitting the model, we standardized all these explanatory variables in Z-values in order to compare the magnitude of their effects, and we performed a Pearson correlation test among them. Explanatory variables were not correlated with each other (p values > 0.1), meaning that the effect of extrinsic and intrinsic variables could be isolated as variables are independent.

Fruit removal was modelled with a binomial distribution where the probability of removal was related via a logit link to plant characteristics:

$$Y_{ij} \sim \text{Binomial}(N_{ij}, p_{ij})$$

$$\text{logit}(p_{ij}) = b_{0j} + b_{1j} \times \text{Accessibility}_{ij} + b_{2j} \times \text{Tree cover}_{ij} + b_{3j} \times \text{LLB}_{1j} + b_{4j} \times \text{Crop size index}_{1j}$$

$$b_{0j} \sim \text{Normal}(\mu_{b0}, \sigma_{b0}^2)$$

$$b_{1j} \sim \text{Normal}(\mu_{b1}, \sigma_{b1}^2)$$

$$b_{2j} \sim \text{Normal}(\mu_{b2}, \sigma_{b2}^2)$$

$$b_{3j} \sim \text{Normal}(\mu_{b3}, \sigma_{b3}^2)$$

$$b_{4j} \sim \text{Normal}(\mu_{b4}, \sigma_{b4}^2)$$

where subscripts *i* and *j* represent each plant and season, respectively; *Y_{ij}* is the number of fruits removed from the plant *i* during season *j*; *b_{0j}* is the intercept, and *b_{1j}*, *b_{2j}*, *b_{3j}*, *b_{4j}* are the coefficients for accessibility, tree cover, LLB, and crop size respectively. We also evaluated first order interactions among explanatory variables (Table A3).

Using a hierarchical model allowed us to evaluate the influence of all covariates in each season and globally, (i.e. the consistency of the effect between seasons). Hierarchical analyses explicitly consider that sampling units have characteristics that differentiate them but also common sources of variation (Gelman and Hill, 2007). Thus, the effect of an environmental variable could be important in a fruiting season but not in another, or it could be important in all seasons. If the effect of a variable is consistent across seasons, it highlights the importance of this environmental feature in the removal process. We fitted the model employing a Bayesian approach using non-informative priors for all parameters (normal distributions with $\mu = 0$ and $\sigma^2 = 0.0001$). The model was fitted with WinBUGS 1.4 (Bayesian Analysis Using Gibbs Sampler; Lunn et al., 2000). For all model parameters, we used the mean value of posterior distributions as point estimates and the 95% Highest Posterior Density interval (HPD) as measure of uncertainty around point estimates (Gelman and Hill, 2007).

3. Results

3.1. Spatial context and plant characteristics

Tristerix corymbosus individuals were observed in a wide variety of accessibility and tree cover conditions between 0 and 100% (Table 1). LLB varied around 0.53 and 1.9 m (i.e., between 6 and 18 years) in all fruiting seasons (Table 1). Crop size index varied widely among seasons and plants, from 9.18 to 432.27 mean number of fruits per plant (Table 1).

3.2. Fruit removal

At least 60% of the fruits in a plant reached maturity within a season (on average $83\% \pm 5\%$) and only $16\% (\pm 10\%)$ of the fruits

Table 1

General characteristics of the spatial context and *Tristerix corymbosus* individuals in each fruiting seasons.

Season	% Accessibility				% Canopy cover			
	Mean	SD	Min	Max	Mean	SD	Min	Max
2008/2009	60	30	0	100	52	36	0	100
2009/2010	52	22	13	100	52	28	0	90
2010/2011	51	16	13	100	56	17	20	80
2012/2013	65	23	25	100	50	25	10	80

Season	LLB (m)				Crop size index			
	Mean	SD	Min	Max	Mean	SD	Min	Max
2008/2009	1.17	0.22	0.77	1.54	144.12	122.12	17.28	430.9
2009/2010	0.95	0.21	0.53	1.23	48.26	31.76	9.18	138.56
2010/2011	1.1	0.24	0.8	1.53	79.9	64.30	19.11	295.57
2012/2013	1.25	0.28	0.95	1.9	237.46	86.40	133.38	432.27

Note: LLB = length of the longest branch.

overripped per season (Table A1). *Dromiciops gliroides* removed on average 33% ($\pm 5\%$) of the available fruits per season with removal rates ranging between 7% and 52% (Table A1).

Our results showed that accessibility and LLB affected positively *T. corymbosus* fruit removal rate (Table 2 and Fig. 1), and their effect was consistent through all fruiting seasons (Table A2). On average, *D. gliroides* removed 54% more fruits in a plant that had 100% accessibility than in one that had 0% accessibility, and 26% more when LLB was doubled from 0.5 m to 1 m. Highest posterior density interval (HPD) of accessibility and LLB did not include negative values and 98% of their posterior distributions were greater than zero. In contrast, we did not detect any consistent effect of tree cover and crop size index on fruit removal rate (HPD interval included zero and their point estimates were close to zero, Table 2). Even though some seasons presented a positive effect of tree cover (2012/2013) and crop size index (2008/2009) (Table A2), the effect of these variables was not consistent across seasons. We could not detect statistical evidence for first order interactions among explanatory variables consistently among seasons (Table A3), thus we removed them from the model.

4. Discussion

Many studies have shown that several factors can simultaneously affect fruit removal rates (Herrera, 1998; Izhaki, 2002; Jordano, 1987; Morales et al., 2012; Saracco et al., 2005). Both plant traits and their spatial context (i.e. neighbourhood) may influence fruit removal rates (see Sargent, 1990; Saracco et al., 2005; Morales et al., 2012). Here, we sampled plants in a variety of environmental conditions with contrasting crop sizes and ages, and hence, we could quantify the relative effects of extrinsic and intrinsic factors on fruit removal. In this system, where the disperser is an arboreal marsupial, we found that the variables that

Table 2

Global linear model for fruit removal of the mistletoe *Tristerix corymbosus* by the marsupial *Dromiciops gliroides*.

Parameter	Mean	HPD	% PD	n.eff	R.hat
Intercept	-1.14	-2.17, -0.23	0.98	5000	1.01
Accessibility (%)	0.17	0.02, 0.30	0.98	5000	1.04
Tree Cover (%)	0.02	-0.23, 0.27	0.68	5000	1.01
LLB(m)	0.15	0.02, 0.28	0.98	4000	1.00
Crop size index	0.02	-0.58, 0.45	0.59	1200	1.01

Note: HPD = Highest posterior density interval, % PD = Percentage of the posterior distribution greater than 0, n.eff = Effective number of saved simulations for each parameter. R.hat = is the potential scale reduction factor (at convergence, R.hat = 1). LLB = Length of the longest branch.

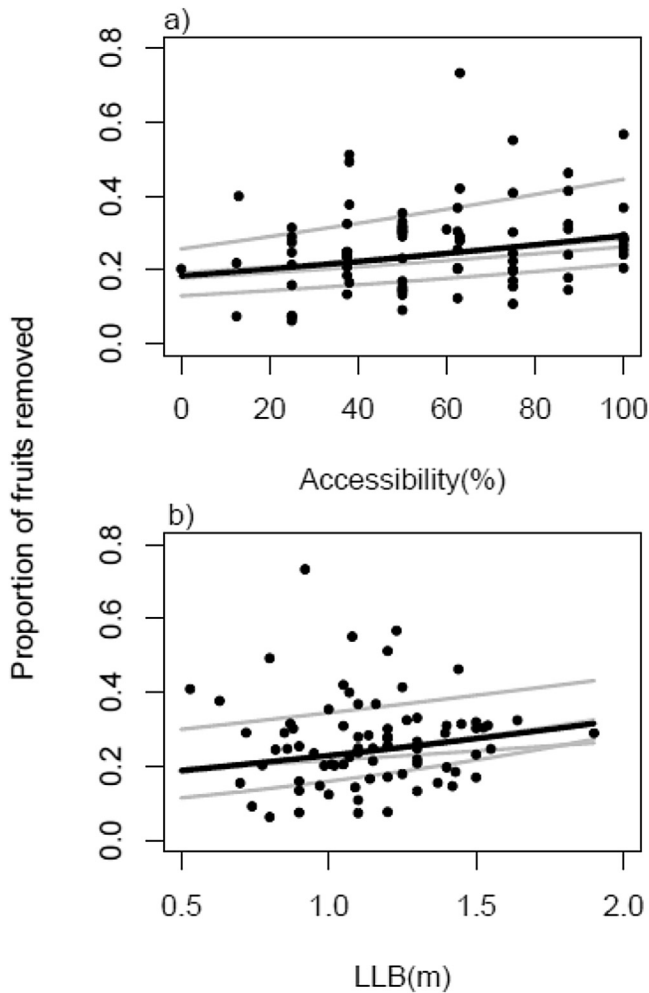


Fig. 1. a) Accessibility and b) LLB (length of the longest branch) effects on fruit removal. Black lines are for the global tendency from a hierarchical binomial regression with accessibility, LLB, crop size index and tree cover as explanatory variables (see data analysis). Grey lines represent the effects for each fruiting season (2008/2009, 2009/2010, 2010/2011, 2012/2013). When plotting the response to a variable we set the remaining tree variables at their average values.

best explained the probability of fruit removal of a particular plant were accessibility and LLB (age).

Each disperser may use and perceive the environment in different ways. Although most frugivorous animals are birds, 20% of terrestrial mammals are partially or mainly frugivorous (Fleming, 1991). For these non-flying frugivores, environmental features associated to their movement and protection may be the most relevant factors affecting fruit consumption. Given that *T. corymbosus* is an arboreal marsupial, it is not surprising that accessibility was one of the variables that best explained fruit removal rates. *D. gliroides* moves through the forest on shrubs and trees branches as well as through dead logs and is highly vulnerable to fragmented habitats (Magrach et al., 2013; Rodríguez-Cabal et al., 2007). Likewise, Fontúrbel et al. (2010) found that this disperser did not use meadows and areas of low shrubs without a tree layer since these areas provide no three-dimensional structure, which facilitates movement and serves as protection against predators. Therefore, given the dispersal service provided by this marsupial to a variety of Patagonian species (Amico et al., 2009), our results highlight the importance of preserving vegetation continuity in order to guarantee the reproductive success of fleshy-fruited plants.

Many authors found that this disperser prefers dense *Nothofagus dombeyi* forests to scrublands or grasslands (Fontúrbel et al., 2010; García et al., 2009; Rodríguez-Cabal and Branch, 2011). In this study, we evaluated the effect of canopy cover at a smaller scale — tree cover at individual plant level — and we did not find any effect on fruit removal. We hypothesized that tree cover would confer protection against predation, but although we found plants in several tree cover conditions (Table 1), in our study site — a dense *Nothofagus dombeyi* forest — canopy cover is mostly high. High canopy cover in our study site may have overridden the effects of tree cover in individual plants. Whether canopy cover at individual plant level affects dispersers' foraging decisions deserves further consideration.

Regarding intrinsic factors, being for a long time in the forest could be an advantage for plants dispersed by animals. As there is a positive relationship between LLB and age (Rodríguez-Cabal et al., 2007), our results show that this disperser prefers older and probably known plants. *D. gliroides* fresh faeces with *T. corymbosus* seeds are usually found next to old ones (from previous seasons), suggesting that this marsupial has movement paths inside the forest that are repeatedly used over the years (Calzolari, 2013). Thus, it is very likely that “known plants” exist along these movement paths. If animals often visit older plants it may be because they are used to them, and they were accessible and safe places to forage in the past.

Despite the fact that we found a positive effect of crop size in fruit removal during the 2008–2009 season (and see Morales et al., 2012; Magrach et al., 2013), the results of several seasons reveal that this effect is not consistent over the years. Given that the spatial structure of mistletoes populations is often aggregated, it may not be the fruit abundance of a particular plant what is attractive for this disperser but the fruit abundance in an area (neighbourhood) (Morales et al., 2012). In mistletoes, local fruit abundance is quite complex to determine as there are several mistletoe individuals per host. A particular plant may have few fruits, but it could share the same environmental characteristics of other plants in the same host which have lots of fruits, which ultimately contribute to the local fruit abundance. Seed dispersal occurs more often towards the host plant or its neighbouring plants, and frequently frugivores deposit more seeds in previously infected hosts or in areas with greater number of mistletoes (Aukema, 2004; Aukema and Martínez del Río, 2002). Therefore, fruit availability in the host plant or in its neighbourhood rather than individual crop size may determine fruit removal (Aukema and Martínez del Río, 2002; Carlo and Morales, 2008).

Animals often make hierarchical decisions to maximize food intake and minimize predation risk (e.g. Fedriani and Boulay, 2006; Sapir et al., 2004). For instance if frugivores satisfied the minimum requirement of the most important factor for them, as crop size (Sapir et al., 2004) or low predation risk (Fedriani and Boulay, 2006), other factors start to play an important role in their decisions. In our study site Rodríguez-Cabal and Branch (2011), in a broader-scale study, found that the factor that best explained *D. gliroides* abundance was *Chusquea couleu* (bamboo) cover, which provides connectivity, refuge and nest-building opportunities. Once the minimum bamboo cover requirement was met, *T. corymbosus* density, which provides food, became important. In our present work, it is possible that only when plant accessibility is already high, *D. gliroides* would then prefer plants with larger fruit crops. In this fashion, when plants extrinsic (spatial context characteristics) rather than intrinsic (plant traits) factors determine fruit removal, they limit the selective pressure exerted by frugivores on plant traits, such as crop or fruit size. A good understanding of frugivores habits is important to predict these hierarchical decisions and to better understand plant-frugivore

interactions and the selection pressures that frugivores may exert on plant traits.

Our findings highlight the importance of studying several seasons in order to make conclusions about the implications that intrinsic and extrinsic factors have on plant–frugivore interactions (Wang and Smith, 2002). Moreover, we show the importance of studying plant–frugivore interactions accounting for spatial structure and plant characteristics. We found, after studying four fruiting seasons, that characteristics associated with frugivores' habits are the most important factors for the reproductive success of plants dispersed by animals.

Authors' contributions

FT, GCA, YS and JMM conceived and designed the study. FT, GCA and YS collected the field data. FT and JMM analysed the data. FT, GCA, YS and JMM interpreted the results, participated in drafting the article and revising the final manuscript.

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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.actao.2017.06.002>.

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