



# 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.

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