Consequences of disperser behaviour for seedling establishment of a mistletoe species

GUILLERMO C. AMICO,* iD YAMILA SASAL, ROMINA VIDAL-RUSSELL, MARCELO A. AIZEN AND JUAN MANUEL MORALES

[1]*Laboratorio Ecotono-INIBIOMA, Conicet- Universidad Nacional del Comahue Bariloche, Río Negro, Argentina (Email: guilleamico@gmail.com)*

Abstract The dispersal process in plants links adults and their offspring. For frugivore-dispersed plants, animal behaviour can have a strong effect on plant fitness. Many mistletoes are totally dependent on animals that deposit seeds on suitable hosts and particular branch diameters. We characterised the seed dispersal and seedling establishment of the mistletoe *Tristerix corymbosus*, which at our study site, is exclusively dispersed by the marsupial *Dromiciops gliroides*. Mistletoes' fruits have a viscous pulp that remains in the seed even after dispersal. This substance adheres the seed to the host branch. We estimated host branch availability in the forest and seed deposition (faeces) by the marsupial in the study area. Specifically, the branch suitability factors we assessed were host identity, branch status (alive or dead), branch diameter, height, and canopy cover. Lodged faeces were individually marked and the number of seed deposited within these droppings was counted, and we recorded the number of seedlings with true leaves that had established after 1 year to estimate the probability of seedling establishment. Branch diameter and canopy cover had a significant positive effect on seed deposition probability. Seedling establishment probability decreased with the number of seeds deposited per faeces and with canopy cover. In general, the marsupial deposited mistletoe seeds in microsites that increase the chance of seedling establishment. Thus, the movement behaviour of the marsupial has a positive effect on the regeneration process of this mistletoe species.

Key words: *Dromiciops gliroides*, parasitic plant, seedling establishment, temperate forest, *Tristerix*.

INTRODUCTION

The dispersal process in plants links adults and their offspring. The majority of tropical and many temperate woody plant species are dispersed by frugivorous animals that eat fruits and defecate or regurgitate seeds (Herrera 2002). The behaviour of animals transporting seeds to specific microsites could greatly affect plant fitness (Russo *et al.* 2006; Schupp *et al.* 2010; Morales *et al.* 2012; Sasal & Morales 2013). Therefore, a central question in the ecology of seed dispersal is to what extent seed dispersers are able to transport seeds to microsites that increase the chance of seedling establishment (Wenny & Levey 1998; Wenny 2001; Cavallero *et al.* 2012). Animal behaviour is particularly critical in plants such as mistletoes (i.e. aerial parasitic plants), where seeds need to be deposited on a suitable host branch for successful seedling establishment (Reid *et al.* 1995; Norton & Reid 1997; López de Buen & Ornelas 2002; Norton *et al.* 2002; Rawsthorne *et al.* 2012). Mistletoes seed dispersers include generalists species and specialists

(Mathiasen *et al.* 2008; Watson & Rawsthorne 2013). Among all microsite factors, the diameter of host branches has been suggested as the most important variable determining mistletoe establishment (Reid 1987, 1989; Sargent 1995; Yan & Reid 1995; Ladley & Kelly 1996; Norton & Ladley 1998).

Mistletoes comprise more of 1400 species of the families Loranthaceae, Viscaceae, Eremopilaceae and Misodendraceae. The vast majority of mistletoe species produce fleshy fruits that are dispersed by animals (Norton & Ladley 1998; Mathiasen *et al.* 2008). Most mistletoe species have been described as dispersed by birds (Reid 1991, Restrepo *et al.* 2002, Watson 2001), but in the temperate forests of Patagonia, the mistletoe *T. corymbosus* is efficiently and almost exclusively dispersed by the marsupial *Dromiciops gliroides* (Amico & Aizen 2000; Amico *et al.* 2011). This endemic arboreal marsupial is also involved in the seed dispersal process of several other plants and it is consider a keystone species in these forests (Amico *et al.* 2009; Rodriguez-Cabal *et al.* 2013). In particular, it has been suggested that seed dispersal by *D. gliroides* plays a crucial role in shaping the spatial structure of the populations of *T. corymbosus* (García *et al.* 2009).

Here, we characterised the seed rain generated by the marsupial *D. gliroides* and the seedling

establishment of the mistletoe *T. corymbosus*. To this end, we compared the characteristics of the substrate where seeds were deposited by the marsupial with respect to substrate availability in the forest. Then, we evaluated factors that affect seedling establishment by comparing the characteristics of the microsites, where seeds were deposited and where seedlings were most likely to survive and establish. Most previous studies of mistletoe establishment have been experimental by "inoculating" seeds on different hosts and branch diameters (Sargent 1995; Norton & Ladley 1998; López de Buen & Ornelas 2002). In this study, we evaluated the processes of seed dispersal, deposition and seedling establishment under natural conditions driven not by the researcher but by the main seed disperser. From a plant perspective, this allowed us to address the adaptive nature of the seed dispersal mutualism.

METHODS

Study area

The study was conducted at the Llao-Llao Forest Reserve, 25 km west of San Carlos de Bariloche, Río Negro, Argentina (41° 8′S, 71° 19′W, 800 m a.s.l.). Native forest vegetation in the area belongs to the Subantarctic biogeographical region (Cabrera & Willink 1980). Dominant canopy trees are the evergreen southern-beech *Nothofagus dombeyi* and the conifer *Austrocedrus chilensis*. The understory includes 15 woody species, but is dominated by the shrub *Aristotelia chilensis* and the bamboo *Chusquea culeou* (ca. 30% and 25% of the total shrub cover, respectively). The two forest layers are well differentiated with tree canopy reaching up to 40 m in height and the understory reaching up to 5 m in height. The climate in this area is cold temperate, with a dry season in spring-summer and a humid season in autumn-winter. On average, only 12% of the annual precipitation (1800 mm) falls during summer (December–February). Snowfalls are common during winter and the annual average temperature is 9°C (Barros *et al.* 1983).

Tristerix corymbosus L. (Kuijt) is the most austral species of the Andean genus *Tristerix,* which comprises 11 species (Kuijt 1988; Amico *et al.* 2007). *Tristerix corymbosus* has a latitudinal range of more than ten degrees, from La Serena (30° 33′S) in the North to Chiloe island (42° 42′S) in the South (Kuijt 1988; Amico *et al.* 2011). The distribution of *T. corymbosus* spans two distinct biomes: the Chilean matorral in the North of its range to temperate forest in the South. This winter-flowering mistletoe produces red tubular hermaphroditic flowers (ca. 5 cm long) that are pollinated mainly by the austral hummingbird *Sephanoides*

sephaniodes (Aizen 2003). The one-seeded fruits are ca. 0.9×0.6 cm and the seeds (ca. 0.6 cm long) are surrounded by a viscous pulp. In the Chilean Matorral, there are three bird species, the white-crested elaenia (*Elaenia albiceps*) the Chilean mockingbird (*Mimus thenca*) and the austral thrush (*Turdus falcklandii*) that disperse its seeds; while in the temperate forest, the sole disperser is the marsupial *Dromiciops gliroides* (Amico *et al.* 2011). Mistletoe seeds of *Tristerix* germinate immediately after they are deposited. The cotyledonary petioles are fused and elongate towards the host; the short radicle produce a disc like swelling that penetrates the host to initiate the infection. The radicle and the fused cotyledonary petioles are evident 2–3 days after seed deposition. *Tristerix corymbosus* parasitises more than 25 species throughout its geographical range (Amico 2007). However, in the study site, the most frequent host are the shrubs *A. chilensis* (76%), *Azara microphylla* (21%) and *Maytenus boaria* (3%) (García *et al.* 2009). Secondary dispersal or post-dispersal seed predation has not been observed for this species.

Host branch availability in the forest

To quantify vegetation structure and composition in the study area, in December 2000 and 2010, we established five linear parallel transects each 500-m long. The transects were separated from each other by at least 30 m. Along each transect, we recorded all plant stems that intercepted a 3 m vertical pole. The variables measured for each interception point were plant species, branch status (dead or alive), branch diameter, height above ground, and canopy cover. Branch diameter was measured with a calliper to 0.1 mm, height with a measuring tape to 0.1 m and canopy cover (percentage) immediately above the intercept point was visually estimated. We measured vegetation structure up to 3 m because the activity of the marsupial is restricted mainly to the forest understory layer (<3 m from the ground) (Calzolari 2013).

Seed dispersal and seedling establishment

The presence of dispersed mistletoe seeds can be accurately determined by carefully inspecting the shrub branches for marsupial faeces. *Tristerix corymbosus* seeds are relatively large (6 mm in length) and white, making them easily distinguishable from the dark branches of the host shrubs. We carried out a systematic survey looking for fresh marsupial faeces containing dispersed mistletoe seeds during the fruiting seasons (from December to April) of 2000–2001 and 2010–2011. Every 2 weeks, we recorded all new faeces found with *T. corymbosus* seeds within the 4-ha plot, where we placed the vegetation transects 3 m height.

For each faecal clump found, we counted the number of *T. corymbosus* seeds, and measured the same variables we recorded during the host branch availability survey (i.e. branch identity and status, diameter, and height above ground, and canopy cover). All faecal clumps were individually marked with a numbered tag. We checked and recorded the number of seedlings with true leaves after 1 year for both sampling seasons.

Data analysis

We modelled the probability of seed deposition by logistic regression models that compared the data on the branches, where faeces containing seeds were found vs. the data on branch characteristics in the forest. The explanatory variables used were: host species identity, branch status, branch diameter, height above ground, and canopy cover. The model also included the squared of the variables branch diameter, height and canopy cover to detect possible non-linear effects. The most common plant species (>5% of the observations) were included in the model, while the rest were grouped as "other species". We were interested in whether the coefficients for the explanatory variables were significantly different from zero and computed confidence intervals from likelihood profiles.

We estimated the probability of seedling establishment per deposition as the number of seedlings established from the number of seeds deposited. The model was fitted for the most common host, *A. chilensis,* (*n* = 441); the other two host species, *Maytenus boaria* (*n* = 9) and *Azara microphylla* (*n* = 4), were discarded due to low sample size. We built a binomial regression model with seedling establishment probability as the response variable and branch diameter, height above ground, forest cover and numbers of seeds per faeces as explanatory variables. All variables recorded (branch diameter, height above ground and canopy cover) showed similar patterns across the two seasons, with no statistical interannual differences (all *P* values >0.10) for any of the variables and are analysed together. The variables were standardised (each value subtracted from the mean and divided by the standard deviation) and the standardised branch diameter was log transformed prior to analysis. All regression models were fitted using package bbmle (Bolker 2010) in R (R Core Team 2016).

RESULTS

Host branch availability in the forest

We measured the branch and plant characteristics at a total of 1129 interception points along the five transects. In total, we found 20 different plant species, of which *A. chilensis* (61%) and *C. culeou* (11%) were the most common. For *A. chilensis*, 34% were dead branches. The intercepted branch diameters varied between 0.1 and 55 cm (mean ± SD, 1.41 ± 2.12 cm). Nearly, 70% of the branches had diameters <1.5 cm. The heights of the branches intercepted varied between 0.05 and 3 m above ground (1.53 ± 0.68 m). More than 75% of the intercepted branches were found <2 m above the ground. Forest cover varied between 0 and 100% (49.61 ± 28.60%). Sixty per cent of the observations had tree cover ranges between 50 and 80%. In summary, branches in the forest are mostly available within the first 2 m above the ground, they are relatively thin (<1.5 cm in diameter), slightly over half belong to the species *A. chilensis*, and the canopy cover was commonly more than 50%.

Faecal deposition and seed dispersal

We found 280 and 250 faecal clumps in 2000–2001 and 2010–2011, respectively, containing a total of 1985 seeds. The number of seeds per clump varied from 1 to 14 (mean ± SD, 3.72 ± 2.21); however, 65% had between 1 and 4 seeds. We recorded faeces on a total of 10 different plant species; however, 88% were found on branches of *A. chilensis*. 87% were found on living branches and only 13% on dead branches of this host species. Faeces were also found on established mistletoe branches (*n* = 18), on *Schinus patagonicus* (*n* = 13), on *Maytenus boaria* (*n* = 9), on *Azara microphylla* (*n* = 4) and on other five species. Faeces were deposited on branches with diameters varying between 0.1 and 9 cm (2.71 ± 1.57 cm). About 75% of the faeces were deposited on branches with diameters between 1 and 5 cm. Faeces were found between 0.15 and 3 m above the ground (mean = 1.53, SD ± 0.38). More than 60% were located at a height between 1 and 2 m. The forest cover above each faecal clump varied between 0 and 100% (mean = 62.03, SD ± 21.47). Seventy per cent of the faeces had been deposited on branches with high canopy cover (> 50%). In summary, mistletoe seeds were mostly defecated onto branches of *A. chilensis* that were 1–5 cm in diameter, were located at 1–2 m above ground with canopy cover higher than 50%.

Seed deposition probability

The logistic regression of seed deposition indicated a significant effect of branch diameter, branch height, and canopy cover (Table 1). Branch diameter had a positive effect on seed deposition (Fig. 1a). Height

Table 1. Probability of mistletoe seed deposition as a function of branch characteristics. Estimates, standard errors, z-value and significance for the faeces deposition model as a function of branch diameter, height above ground, canopy cover and host identity are shown.

	Estimate	SE	z-value	Pr(z)
Intercept	−2.445	7.156	−0.341	0.732
Branch diameter	1.324	0.092	14.252	<0.001***
Branch diameter^2	−0.202	0.071	−2.854	0.004*
Height	0.049	0.094	0.528	0.597
Height^2	−0.876	0.089	−9.806	<0.001***
Canopy cover	0.204	0.081	2.502	0.012*
Canopy cover^2	−0.111	0.074	−1.502	0.133
Aristotelia chilensis	2.894	7.156	0.404	0.685
Dead branches	1.555	7.157	0.217	0.827
Chusquea culeou	−9.186	42.92	−0.214	0.830
Nothofagus dombeyi	−1.127	7.207	−0.156	0.875
Schinus patagonicus	0.971	7.161	0.135	0.892
Other substrate	2.446	7.158	0.341	0.732

*$P < 0.05$, ***$P < 0.001$.

showed no linear effect, but a significant quadratic effect, indicating seed deposition across an optimal range of heights (Fig. 1b). Canopy cover had a positive linear effect on seed deposition (Fig. 1c). Host species had no significant effect on seed deposition probability (Table 1).

Seedling establishment

Seedling status was recorded after 1 year for both sampling seasons. A total of 128 faecal clumps (24%) had at least one seed from which a seedling became established. Mistletoe seeds became established mostly in *A. chilensis* ($n = 115$), and less commonly in *Maytenus boaria* ($n = 4$) and *Azara microphylla* ($n = 1$). None was recorded in *C. culeou*. The proportion of established seedlings (number of seedlings/total of seeds) was 0.11. The mean number of seedlings per clump was 1.58 ($\pm$ 0.89). Seedling establishment on *A. chilensis* indicated a significant negative effect of number of seeds per faecal and of canopy cover (Table 2, Fig. 2). The other two variables, branch diameter and height, had no detectable effect on seedling establishment.

DISCUSSION

The quality of seed dispersal affects the probability that seeds will reach the adult stage, and thus, animals that efficiently disperse seeds contribute to

overall plant fitness (Wenny & Levey 1998; Wenny 2001; Schupp *et al.* 2010). Mistletoes, such as the *Tristerix* studied here, require an animal vector for seed dispersal to an appropriate host and also to a suitable branch within the host. In general, we found that the marsupial *Dromiciops gliroides* deposited seeds of *T. corymbosus* at microsites, where establishment probability was quite high. Therefore, the behaviour of the marsupial dispersing *T. corymbosus* seeds favours the regeneration of this mistletoe species.

Seed deposition patterns

The marsupial deposited most mistletoe seeds on *A. chilensis* branches ranging between 1 and 5 cm in diameter, according to data gathered from the faecal survey. Available branches in the forest averaged, 15 mm in diameter; however, *D. gliroides* deposits seeds on branches with a larger average than this (27 mm). The usual branch diameter where this marsupial deposits seeds is considerably greater than that reported by birds of other mistletoe species. For example, in the Australian mistletoe *Amyema quandang* (Loranthaceae), most seeds were deposited on branches <10 mm by two bird species (Reid 1989). Thus, deposition on thicker branches may be a consequence of dispersal by mammals vs. birds rather than a reflection of branch availability.

The height of branches above ground also affected the probability of seed deposition by the marsupial. The seed disperser deposited seeds within a height range lower than that available in the forest. More than 60% of faeces were deposited 1–2 m above ground. This deposition range represents an intermediate height of the understory vegetation. For bird-dispersed mistletoes, it has been reported that seed deposition usually occurs in the tree canopy (Aukema & Martínez del Rio 2002a; Amico *et al.* 2011). This difference may be due to the behaviour of the marsupial that prefers to move at intermediate heights of the understory, where the vegetation is more continuous (Calzolari 2013). Also, this difference could be associated with a lower risk of predation at the intermediate understory vegetation.

Canopy cover had a positive effect on the probability of seed deposition, that is, seeds were more likely to be deposited under a dense canopy cover. Probably, the marsupial is selecting sites with high canopy cover to avoid predation (Rodriguez-Cabal & Branch 2011). This aspect of the marsupial behaviour does not favour seed establishment of the mistletoe since the canopy cover had a negative effect on mistletoe establishment.

In our study site, substrate type had no significant effect on seed deposition probability. The majority of faecal masses with mistletoe seeds (77%) were
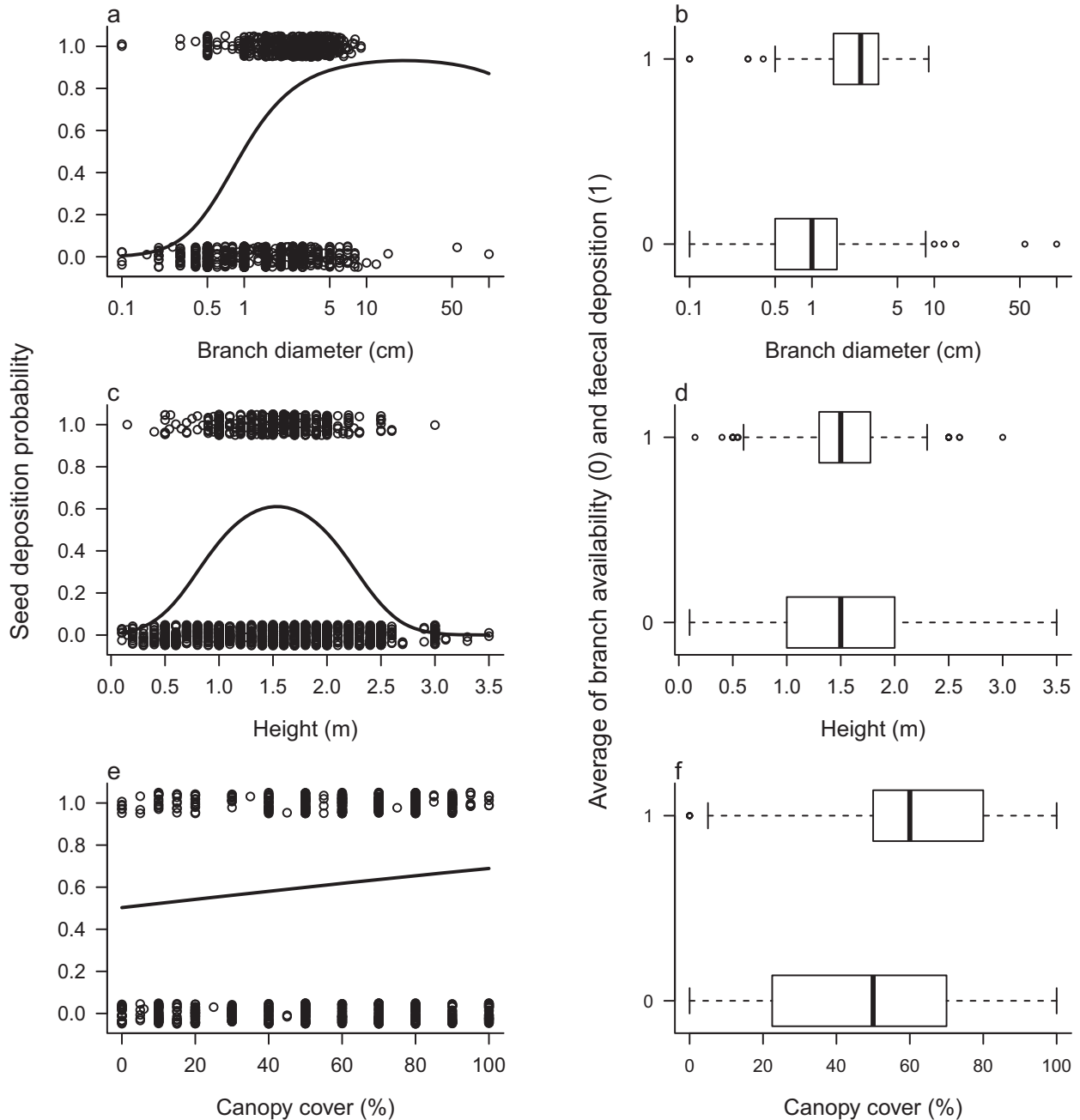
Fig. 1. Deposition probability and box plots of mistletoe seeds in relation to branch diameter (a, b), height (c, d) and canopy cover (e, f). The points on the Y axis equal to 0 (zero) represent the observations of host branch availability in the forest and equal to 1 (one) represent faecal deposition by the marsupial. Because there are many values at the same value of Y, we use jitter function to spread them out in figure a, c and e. The curve in figure a, c and c represent how the relative probability of use changes as a given variable changes and the others variables remain at their average value.

deposited on living branches of the main host (*A. chilensis*), but this was also the most common stem in the forest (61%). For other mistletoe species, it has been reported that most seeds are deposited on previously infected host plants (Aukema 2004; Rawsthorne *et al.* 2012). For *T. corymbosus*, more than 55% of the faecal masses were deposited on uninfected hosts (Amico 2000). In spite of no significant effect of substrate type on seed deposition, the marsupial is favouring mistletoe survival in the forest by depositing seeds on suitable hosts and often on noninfected hosts.

Table 2. Mistletoe seedling establishment. Estimates, standard errors, z-value and significance for the model of seed establishment as a function of branch diameter, number of other seeds per dropping, height above ground and canopy cover.

	Estimate	SE	z-value	Pr (z)
Intercept	−1.039	0.259	−4.009	<0.001***
Branch diameter	0.003	0.079	0.039	0.968
Branch diameter^2	0.037	0.048	0.775	0.438
Number of seeds	−0.251	0.098	−2.570	0.010*
Number of seeds^2	0.007	0.009	0.816	0.414
Height	−0.050	0.069	−0.734	0.462
Height^2	0.057	0.039	1.429	0.152
Canopy cover	−0.167	0.080	−2.067	0.038*
Canopy cover ^{2}	0.0153	0.049	0.315	0.752

*P < 0.05, ***P < 0.001.

Seedling establishment

In this study, we found that *Dromiciops gliroides* dispersed most seeds on *A. chilensis* where establishment was successful. Fewer numbers of seeds were deposited on other viable hosts (*Maytenus boaria* and *Azara microphylla*) in the study area. It would be necessary to perform seed inoculations on different hosts to evaluate the potential establishment success in species other than *A. chilensis*.

Seedling establishment of other mistletoe species has been shown to be affected by branch diameter (Sargent 1995; Norton & Ladley 1998; López de Buen & Ornelas 2002). However in our study system, we have not found an effect of branch size on seedling establishment. The marsupial deposited most seeds on branches 1–5 cm and successful seed establishment occurred over the whole of this range of branch diameters. Seedling establishment for most mistletoe species occurs most commonly on thin branches. About 50% of the seeds of the New Zealand mistletoe *Alepis flavida* (Loranthaceae) successfully established a seedling when placed on small branches (<50 mm) of its host *Nothofagus solandri* (Norton & Ladley 1998). For two *Amyema* species of eastern Australia, maximum establishment occurred on branches of 7–20 mm (Yan & Reid 1995). For *Psittacanthus schiedeanus* (Loranthaceae) of Mexico, establishment was higher on branches <5 mm in diameter (López de Buen & Ornelas 2002). For *Phoradendron robustissimum* (Viscaceae) in Costa Rica, seedling establishment was more frequent on branches of *Sapiumo ligoneuron* (Euphorbiaceae) 1–14 mm in diameter (Sargent 1995). Hence, *T. corymbosus* can establish on a wider range of diameters and even on more lignified host branches than other mistletoes that have been studied previously. On the other hand, the lack of effect of branch diameter on the seedling establishment model
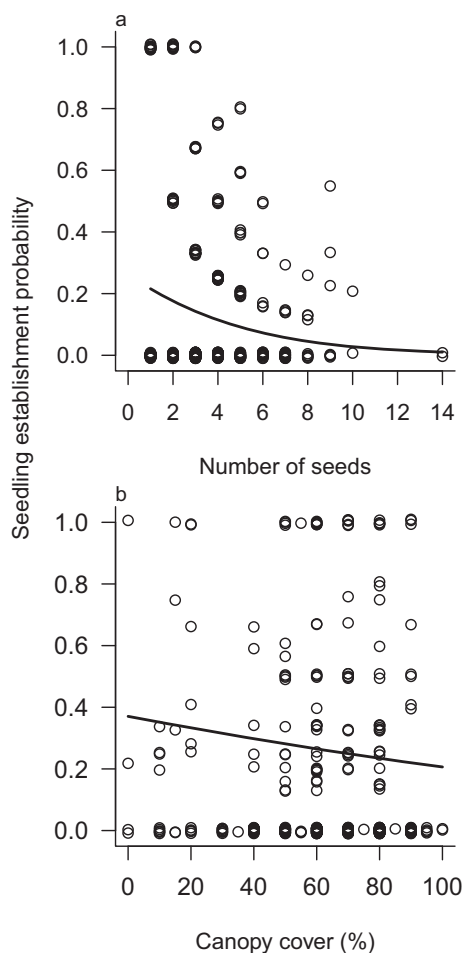

Fig. 2. Establishment probability of mistletoe seedlings in relation to the number of seed deposited per faeces (a) and canopy cover (b).

indicates that the marsupial is depositing seeds over a range of branch sizes where they can establish.

Canopy cover influence the establishment and survival of mistletoe seedlings in varying ways (López de Buen & Ornelas 2002; Mellado & Zamora 2014). We found that *T. corymbosus* establishment was higher in areas with low canopy cover, and thus with more light. This is in agreement with other Loranthaceae species of Mexico, *Psittacanthus schiedeanus* (López de Buen & Ornelas 2002). But for a species of Mediterranean pine-forest (*Viscum album* -Viscaceae) a positive effect of seedling establishment and canopy cover was reported (Mellado & Zamora 2014). Despite the favourability of high light environments for seedling establishment of *T. corymbosus*, the marsupial tended to deposit seeds in areas with high canopy cover but not exclusively so – there is a broad range of cover in deposited sites. Thus, the behaviour of the seed disperser is not always favouring the establishment in terms of canopy cover. However, canopy cover is the

only aspect of marsupial behaviour that is not favourable to mistletoe seedling establishment. For all the other variables considered in this study (branch diameter, height, and host species), the marsupial deposited seeds where they had high probability of establishment either due to habitat use selectivity (e.g. branch diameter) or not (e.g. host identity).

In many plants, the presence of multiple seeds per faecal mass (clumping) has a detrimental effect on seedling survival (Howe 1989). In other mistletoe species, as well as *T. corymbosus* reported here, the number of the seeds per faecal mass negatively influenced the likelihood of each seedlings establishing (Davidar 1983, Larson 1991, but see Sargent 1995; Kelly *et al.* 2007). The number of seeds per faecal mass in *T. corymbosus* deposited by the marsupial in the forest was significantly higher than masses dispersed by birds in the Chilean matorral (Amico *et al.* 2011). This is despite the fact that the marsupial tends to defecate seeds continually while wandering over the branches, and not in clumps of seeds from a sedentary position. In contrast, most bird species generate seed clumps by depositing seeds on certain individual plants, perches or dead branches (Aukema & Martínez del Rio 2002b; Amico *et al.* 2011; Rawsthorne *et al.* 2012) generating a clump of seeds. In the Chilean matorral, birds were less effective seed dispersers of *T. corymbosus* than the marsupial because they deposited more seeds on dead branches and also on the ground (Amico *et al.* 2011).

Establishment of *T. corymbosus* was favoured by the behaviour of the marsupial. Seeds were deposited in suitable hosts, and at adequate branch sizes. The only downside was that the marsupial deposited seeds mostly at high canopy cover where seeds had lower probability of establishment. However, this has no negative effect in the overall dynamic of the mistletoe in the forest. The relationship between marsupial and mistletoe affects positively the regeneration process of this plant species in the forest. This system, mistletoe-marsupial, thus represents another case of direct dispersal, reported for tropical forests plants and mistletoes (Wenny & Levey 1998; Wenny 2001).

AUTHOR CONTRIBUTIONS

GCA and MAA conceived and designed the experiments. GCA, YS and RVR performed the experiments. GCA, YS, JMM analysed the data. GCA, YS, RVR, MMA and JMM wrote the manuscript.

REFERENCES

Aizen M. A. (2003) Influences of animal pollination and seed dispersal on winter flowering in a temperate mistletoe. *Ecology* **84,** 2613–27.

Amico G. C. (2000) Dispersión del quintral (*Tristerix corymbosus*) por el Monito del Monte (*Dromiciops australis*) (Licenciatura Thesis). Universidad Nacional del Comahue, Bariloche, RN Argentina.

Amico G. C. (2007) *Variación Geográfica en la Coloración de los Frutos del Muérdago Tristerix Corymbosus* (Loranthaceae): Efecto de la Historia Evolutiva, del Ambiente, de los Dispersores de Semillas y de los Hospedadores (PhD Thesis). Universidad Nacional del Comahue, Bariloche, RN, Argentina.

Amico G. C. & Aizen M. A. (2000) Mistletoe seed dispersal by a marsupial. *Nature* **408,** 929–30.

Amico G. C., Vidal-Russell R. & Nickrent D. (2007) Phylogenetic relationships and ecological speciation in the mistletoe *Tristerix* (Loranthaceae): the influence of pollinators, dispersers, and hosts. *Am. J. Bot.* **94,** 558–67.

Amico G. C., Rodrigues-Cabal M. & Aizen M. A. (2009) The potential key seed-dispersing role of the arboreal marsupial *Dromiciops gliroides. Acta Oecol.* **35,** 8–13.

Amico G. C., Rodriguez-Cabal M. A. & Aizen M. A. (2011) Geographic variation in fruit colour is associated with contrasting seed disperser assemblages in a south-Andean mistletoe. *Ecography* **34,** 318–26.

Aukema J. E. (2004) Distribution and dispersal of desert mistletoe is scale-dependent, hierarchically nested. *Ecography* **27,** 137–44.

Aukema J. E. & Martínez del Rio C. (2002a) Variation in mistletoe seed deposition: effects of intra- and interspecific host characteristics. *Ecography* **25,** 139–44.

Aukema J. E. & Martínez del Rio C. (2002b) Where does a fruit-eating bird deposit mistletoe seeds? Seed deposition patterns and an experiment. *Ecology* **83,** 3489–96.

Barros V. R., Cordon V., Moyano C., Méndez R., Forquera J. & Pizzio O. (1983) *Cartas de Precipitación de la Zona Oeste de las Provincias de Río Negro y Neuquén.* Facultad de Ciencias Agrarias, Universidad Nacional del Comahue Cinco Saltos, Cinco Saltos, Argentina.

Bolker B. (2010) bmle: Tools for general maximum likelihood estimation. R package version 0.9.

Cabrera A. L. & Willink A. (1980) *Biogeografía de América Latina.* Secretaría General de la Organización de los Estados Americanos, Washington, DC.

Calzolari G. (2013) Uso de micro-hábitats por el monito del monte (*Dromiciops gliroides*) y posibles consecuencias para la dinámica del quintral (*Tristerix corymbosus*) (Licenciatura Thesis). Universidad Nacional del Comahue, Bariloche.

Cavallero L., Aizen M. A. & Raffaele E. (2012) Endozoochory decreases environmental filtering imposed to seedlings. *J. Veg. Sci.* **23,** 677–89.

Davidar P. (1983) Birds and neotropical mistletoes: effects on seedling recruitment. *Oecologia*, **60,** 271–3.

García D., Rodríguez-Cabal M. A. & Amico G. C. (2009) Seed dispersal by a frugivorous marsupial shapes the spatial scale of a mistletoe population. *J. Ecol.* **97,** 217–29.

Herrera C. M. (2002) Seed dispersal by vertebrates. In: *Plant-Animal Interactions: An Evolutionary Approach* (eds C. M. Herrera & O. Pellmyr) pp. 185–208. Blackwell, Oxford, UK.

Howe H. F. (1989) Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* **79,** 417–26.

Kelly D., Ladley J. J. & Robertson A. W. (2007) Is the pollen-limited mistletoe *Peraxilla tetrapetala* (Loranthaceae) also seed limited? *Austral Ecol.* **32,** 850–7.

Kuijt J. (1988) Revision of *Tristerix* (Loranthaceae). *Syst. Bot. Monogr.* **19,** 61.

Ladley J. J. & Kelly D. (1996) Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): dependence on birds. *N. Z. J. Ecol.* **20,** 69–79.

Larson D. L. (1991) *Ecology of desert mistletoe seed dispersal*. PhD Thesis, University of Illinois at Chicago, Chicago.

López de Buen L. L. & Ornelas J. F. (2002) Host compatibility of the cloud forest mistletoe *Psittacanthus schiedeanus* (Loranthaceae) in Central Veracruz, Mexico. *Am. J. Bot.* **89,** 95–102.

Mathiasen R. L., Nickrent D. L., Shaw D. C. & Watson D. M. (2008) Mistletoes: pathology, systematics, ecology, and management. *Plant Dis.* **92,** 988–1006.

Mellado A. & Zamora R. (2014) Linking safe sites for recruitment with host-canopy heterogeneity: The case of a parasitic plant, *Viscum album* subsp. *austriacum* (Viscaceae). *Am. J. Bot.* **101,** 957–64.

Morales J. M., Rivarola M. D., Amico G. C. & Carlo T. A. (2012) Neighborhood effects on seed dispersal by frugivores: testing theory with a mistletoe-marsupial system in Patagonia. *Ecology* **93,** 741–8.

Norton D. A. & Ladley J. J. (1998) Establishment and early growth of *Alepis flavida* in relation to *Nothofagus solandri* branch size. *NZ J. Bot.* **36,** 213–17.

Norton D. A. & Reid N. (1997) Lessons in ecosystem management from management of threatened and pest loranthaceous mistletoes in New Zealand and Australia. *Conserv. Biol.* **11,** 759–69.

Norton D. A., Ladley J. J. & Sparrow A. D. (2002) Host provenance effects on germination and establishment of two New Zealand mistletoes (Loranthaceae). *Funct. Ecol.* **16,** 657–63.

R Core Team (2016) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Rawsthorne J., Watson D. M. & Roshier D. A. (2012) The restricted seed rain of a mistletoe specialist. *J. Avian Biol.* **43,** 9–14.

Reid N. (1987) Safe sites for *Amyema quandang* (Lindl.) van Tiegh. (Loranthaceae) seeds: Dispersal requirements and post-dispersal mortality. In: *Proceedings of the 4th International Symposium on Parasitic Flowering Plants; August 1987, Marburg* (eds H. C. Weber & W. Forstreuter) pp. 691–9. Philipps-Universität, Marburg.

Reid N. (1989) Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. *Ecology* **70,** 137–45.

Reid N. (1991) Coevolution of mistletoes and frugivorous birds? *Aust. J. Ecol.* **16,** 457–69.

Reid N., Stafford M. & Yan Z. (1995) Ecology and population biology of mistletoe. In: *Forest Canopies* (eds M. D. Lowman & M. M. Nadkarni) pp. 285–310. Acadamic Press, Orlando, FL.

Restrepo C., Sargent S., Levey D. J. & Watson D. M. (2002) The role of vertebrates in the diversification of New World mistletoes. In: *Seed dispersal and frugivory: ecology, evolution and conservation* (eds D. J. Levey, W. R. Silva & M. Galetti) pp. 83–98. CAB International, Wallingford, UK.

Rodriguez-Cabal M. A. & Branch L. C. (2011) Influence of habitat factors on the distribution and abundance of a marsupial seed disperser. *J. Mammal.* **92,** 1245–52.

Rodriguez-Cabal M. A., Barrios-Garcia M. N., Amico G. C., Aizen M. A. & Sanders N. J. (2013) Node-by-node disassembly of a mutualistic interaction web driven by species introductions. *Proc. Natl. Acad. Sci. USA* **110,** 16503–7.

Russo S. E., Portnoy S. & Augspurger C. K. (2006) Incorporating animal behavior into seed dispersal models implications for seed shadows. *Ecology* **87,** 3160–74.

Sargent S. (1995) Seed fate in a tropical mistletoe: the importance of host twig size. *Funct. Ecol.* **9,** 197–204.

Sasal Y. & Morales J. M. (2013) Linking frugivore behavior to plant population dynamics. *Oikos* **122,** 95–103.

Schupp E. W., Jordano P. & Gómez J. M. (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytol.* **118,** 333–53.

Watson D. M. (2001) Mistletoe – a keystone resource in forests and woodlands worldwide. *Annu. Rev. Ecol. Evol. Syst.* **32,** 219–49.

Watson D. M. & Rawsthorne J. (2013) Mistletoe specialist frugivores: latterday 'Johnny Appleseeds' or self-serving market gardeners? *Oecologia* **172,** 925–32.

Wenny D. G. (2001) Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evol. Ecol. Res.* **3,** 51–74.

Wenny D. G. & Levey D. J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. *Proc. Natl. Acad. Sci. USA* **95,** 6204–7.

Yan Z. G. & Reid N. (1995) Mistletoe (*Amyema miquelii* and *A. pendulum*) seedling establishment on eucalypt hosts in eastern Australia. *J. Appl. Ecol.* **32,** 778–84.