BIOLOGICAL CONSERVATION

Habitat fragmentation disrupts a plant-disperser mutualism in the temperate forest of South America

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ABSTRACT

The disruption of dispersal mutualisms may have profound consequences for seedling recruitment, plant demography, and population persistence, with potential cascading effects throughout the rest of the community. In the temperate forest of South America, the seeds of the mistletoe *Tristerix corymbosus*, a proposed key species, are dispersed solely by the endemic marsupial *Dromiciops gliroides*. In three sites that included two contrasting habitats, one fragmented and the other not, we assessed effects of forest fragmentation on marsupial abundance, fruit removal, seed dispersal and seedling recruitment rates. We also compared the age structure of mistletoe populations between fragmented and non-fragmented forest habitats. Fragmentation affected negatively marsupial abundance, fruit removal, seed dispersal, and seedling recruitment. The local extinction of *D. gliroides* was associated with the complete disruption of mistletoe seed dispersal. Mistletoe populations in fragmented forests exhibited a deficiency in juveniles because of a lack of recruitment. Thus, effects of forest fragmentation on this dispersal mutualism have clear demographic consequences, which may compromise the survival of mistletoe populations.

1. Introduction

Plant–animal mutualisms, including pollination and seed dispersal, are essential interactions not only for the persistence of mutualistic partners, but also for biodiversity maintenance and ecosystem integrity (Tabarelli et al., 1999; Traveset, 1999; Christian, 2001; Cagnolo et al., 2006). The disruption of pollination and seed dispersal mutualisms can affect sexual reproduction, patterns of gene flow, plant recruitment and population demography, other interspecific interactions, and also species potential for evolutionary change (Wilson et al., 1995).

Fragmentation and, more generally, alteration of natural habitats due to human activities can have profound effects on species interactions due to local extinctions and/or replacement of interactive partners (Kareiva, 1987; Saunders et al., 1991; Aizen and Feinsinger, 1994a,b; Esseen, 1994; Santos and Tellería, 1994; Santos et al., 1999). In turn, the disruption of these interactions, particularly of plant–animal mutualisms, may cascade through the community increasing extinction rates of species directly or indirectly involved in these relationships (Aizen and Feinsinger, 1994a; Bond, 1994; Harrison and Bruna, 1999; Traveset and Riera, 2005). Particularly, these cascading effects may worsen when the affected mutualists are also keystone species. Despite the ecological importance of these species, and of the interactions they are involved in, fragmentation studies focused on keystone mutualists are rare.

Here we assess effects of forest fragmentation on seed dispersal of the mistletoe *Tristerix corymbosus* (L.) Kuijt, a keystone species from the temperate forest of South America. This plant species represents the main, and in some regions the sole winter nectar source for *Sephanoides sephaniodes* Gray (Aizen, 2003), the only year-round resident hummingbird in this forest and responsible for the pollination of nearly 20% of the highly endemic woody flora of this biome (Smith-Ramirez, 1993; Armesto et al., 1996; Aizen and Ezcurra, 1998; Aizen et al., 2002).

Because of its aerial parasitic habit, seed dispersal represents a critical step in a mistletoe life cycle. Thus, it is not surprising that dispersal of mistletoe seeds is usually carried out by specialized birds (Reid, 1991). In the temperate forest of southern South America, however, the seeds of *T. corymbosus* are exclusively and efficiently dispersed by the marsupial *Dromiciops gliroides* Philippi (Amico and Aizen, 2000; Aizen, 2003).

This marsupial consumes massive amounts of *T. corymbosus* fruits during the austral summer, ingesting and defecating the soft mistletoe seeds undamaged. In addition, most defecated seeds are stuck to branches and the passage through the marsupial's gut is crucial to trigger germination (Amico and Aizen, 2000). *D. gliroides* is considered a true living fossil (Marshall, 1978; Kelt and Martínez, 1989; Spotorno et al., 1997; Springer et al., 1998), and this mistletoe–marsupial dispersal interaction might represent a very ancient mutualism that could have preceded the origin of more widespread mistletoe-bird dispersal (Amico and Aizen, 2000). Given the high dependence of the mistletoe on *D. gliroides* for seed dispersal, the disruption of this mutualistic interaction might have direct implications for the survival of *T. corymbosus* populations with ramifying consequences on different components of the biota.

Our specific goals were to determine how forest fragmentation affects: (1) marsupial abundance, (2) fruit removal, (3) seed dispersal, and (4) seedling recruitment. The assessments of all the stages involved in the dispersal process allow us to make strong inference on how human-driven disturbance may influence a highly specialized dispersal interaction. In addition, we compared the age structure of mistletoe populations between fragmented and non-fragmented habitats to evaluate the potential demographic consequences of the disruption of this mistletoe–marsupial mutualism. Here we present results from a field study that strongly suggest that habitat fragmentation has disruptive effects on a keystone interaction for the conservation of the temperate forest of South America.

2.   Materials and methods

This study was carried out in three sites adjacent to Nahuel Huapi National Park, Argentina, in the 2000/2001 austral summer (December–March), the main fruiting and dispersal season of *T. corymbosus* (Aizen, 2003). Mean annual precipitation in the study area is ca. 1800 mm. January and July temperatures average 15 and 3 °C, respectively. Native forest vegetation in the area belongs to the Subantartic biogeographical region (Cabrera, 1976). Dominant trees are the evergreen southern-beech *Nothofagus dombeyi* and the conifer

Austrocedrus chilensis. The understory is dominated by the shrubs *Aristotelia chilensis* and *Maytenus boaria*, the main hosts of *T. corymbosus*, *Azara microphylla* and the bamboo *Chusquea culeou* (Mermoz and Martín, 1986). Introduced plants are also common in the fragmented sites, including *Prunus* sp., *Populus* spp., and scotch broom, *Cytisus scoparius*.

T. corymbosus produces fruits that are green when ripe. Typical of Loranthaceae, each fruit contains only one seed that lacks teguments. When defecated, the sticky pulp surrounding the seed facilitates its attachment to the branch. Seeds can be dispersed singly or more commonly in "necklaces" of up to 20 seeds linked by viscin threads.

This study was carried out in three sites between 18 and 30 km west of the city of San Carlos de Bariloche (41°S, 71°W): Cerro Campanario, Llao-Llao, and Villa Tacul. In each site, we selected two adjacent habitat units, one represented by a mosaic of several forest fragments of 1–5 ha each and the other by a continuous forest >1500 ha that neighbors an extensive forest area protected within the National Park. The two habitat units within a given site were chosen based on similarity in vegetation structure and composition, and the occurrence of a population of *T. corymbosus* with >40 individuals within each habitat unit. Fragments were surrounded by a clearcut matrix, which was periodically brushed and/or mowed. Nearest-neighbor distances between fragments ranged between 60 and 500 m. The two study populations within each site were <1 km apart. Thus, our experimental design involved paired comparisons between mistletoe populations in fragmented and continuous forest habitats.

2.1.   Marsupial abundance

We estimated the abundance of *D. gliroides* by means of live-trapping. We used wire traps (Tomahawk-style) baited with banana and apple, and sampled each habitat unit with 20 traps placed about 5 m apart along a 100 m transect. In the fragmented habitats traps were placed in 2–3 forest fragments. Traps were run over four consecutive days each month from December to March. Traps were checked daily and all trapped marsupials were marked with an individual code based on ear perforations. Marked marsupials were released in the same place where captured (see Wilson et al., 1996).

We used the minimum-number-alive (MNA) index (Conroy, 1996) as an estimator of *D. gliroides* abundance. The lack of recaptures in the fragmented habitats precluded the use of abundance estimators based on capture–recapture methods (Nichols and Pollock, 1983; Nichols and Dickman, 1996) for all habitat units. However, capture–recapture estimates of abundance for the continuous forest units resulted in similar qualitative differences between sites and habitat units as the minimum-number-alive (results not shown).

2.2.   Seed dispersal

In each habitat unit, using small paper tags we marked immature fruits in each of 12 plants chosen at random. At weekly intervals over the sampling period, we recorded the status of each fruit according to one of the following categories: developing fruit, ripe fruit, removed fruit, and senescent

(non-removed) fruit. Ripe fruits are green but soft to the touch. A fruit was considered removed when it was ripe in one census but it was missing in following censuses. Fruits disappearing from the plant when ripe imply animal removal (see Aizen, 2003 for further details). As fruits senesced or were removed, we marked new fruits to monitor a constant number of 20 fruits per plant over the sampling period. Fruit removal was estimated as the percent of all tagged fruits removed over the sampling period. To estimate dispersal rates, we tagged 100 shrubs and tree saplings (DBH < 15 cm) about 2 m apart along a 200 m transect at each site and habitat unit. In the fragmented habitat units, these plant transects encompassed 2–3 forest fragments and overlapped the marsupial-trapping transects. Tagged shrubs included host and non-host plants. We counted the number of reproductive individuals of *T. corymbosus* on the tagged plants and estimated the number of fruits (=seeds) produced by each mistletoe. At weekly intervals, we marked all new feces found on tagged shrubs and counted seeds in each feces. We estimated

dispersal rates as the total number of seeds dispersed found along each transect divided by the total number of fruits produced by the mistletoes present on the transect. This estimation assumes that the number of seeds dispersed from mistletoes occurring on tagged shrubs to surrounding non-tagged shrubs was similar to the number of seeds dispersed from mistletoes on surrounding non-tagged shrubs to the shrubs tagged along each transect. Although this assumption may not be necessarily true, these dispersal estimates should not be biased by habitat type and thus they are useful for comparative purposes.

2.3. Seedling establishment and age distribution

We evaluated the effect of habitat fragmentation on seedling establishment over two years. In December (late spring) 2000 and 2001, we counted all new mistletoe seedlings (those presenting the first true two leaves) occurring on the shrubs tagged along each transect. These seedlings established from
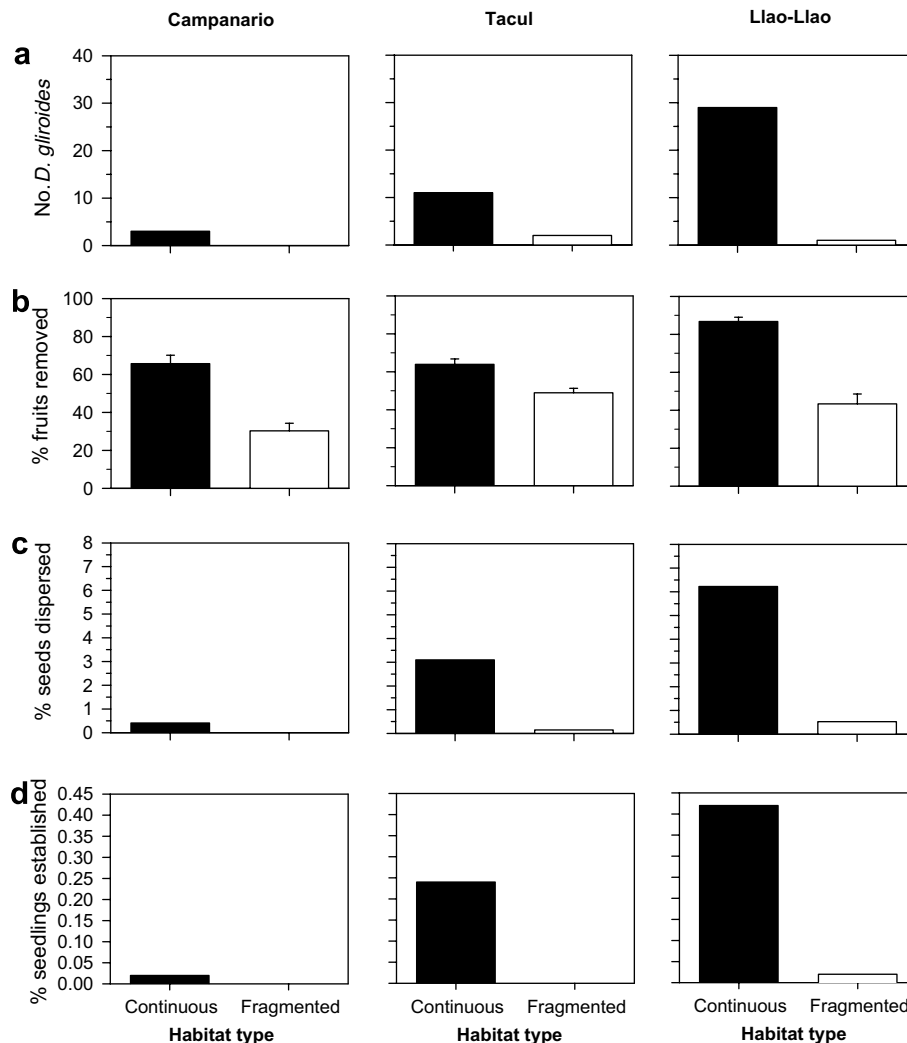

Fig. 1 – Seed dispersal and seedling establishment of *Tristerix corymbosus* in continuous vs. fragmented forest at Campanario, Tacul, and Llao-Llao: (a) minimum number of *Dromiciops gliroides* individuals in each sampled area, (b) number of fruits removed, (c) seeds dispersed, and (d) seedlings established as a percent of the number of fruits (=seeds) produced. In (b), T-bars represent + 1 SE.

the seeds dispersed during the previous fruiting season, austral summers 1999/2000 and 2000/2001, respectively. Seedling establishment was estimated as the (median) number of seedlings per host plant for both 2000 and 2001 seedling counts; and also as a percent of seed production by the focal reproductive mistletoes for the seedlings counted only during 2001, the year we had estimations of seed production.

We studied the age structure of the mistletoe populations occurring in each site and habitat unit. To develop a non-destructive age index, we first collected 40 individual mistletoes, encompassing the range of observed sizes, from different study sites and different hosts. Each *T. corymbosus* individual was harvested along a 5 cm long segment of the host branch centered at the attachment point of the mistletoe. We measured diameter of the mistletoe scar, maximum basal diameter of the mistletoe, diameter of the host branch at the infection, length of the longest mistletoe branch, number of branch tips, maximum branching order, and the length of the infection scar.

We estimated mistletoe age by counting the number of annual growth rings of the host plant at the infection from the host bark to the end of the deepest mistletoe haustorial connection. The accuracy of this method to age mistletoes and a detailed description of the histological procedure we used can be found in Norton et al. (1997). The coefficient of determination (r^2) of the regressions between age and each of the seven morphological variables we measured, ranged between 0.45 and 0.73 (Rodríguez Cabal, 2003). We chose the regression with the best fit, i.e. between age and the length of the longest mistletoe branch, as a non-destructive age estimator (age in years = 0.086 * length in cm + 1.968, $n = 40$, $r^2 = 0.73$). We used this linear equation to estimate the age of all mistletoes (one-yr old seedlings excluded) found on tagged shrubs and treelets at each site and habitat unit.

2.4. Data analysis

We used a paired *t*-test to compare marsupial abundance, number of reproductive mistletoes, fruit production, fruit removal, seed dispersal, and seedling establishment between fragmented and non-fragmented habitat units considering each site as a replicate (i.e., two degrees of freedom). Excluding the number of reproductive mistletoes and fruit production per mistletoe and transect, these tests were one-tailed because of the hypothetical disruptive effect of habitat fragmentation on the dispersal process. In addition, because of the logistic difficulties to achieve high replication in this type of conservation studies we used a more liberal significance level of $\alpha = 0.10$ (Vázquez and Simberloff, 2004). In any event, we combined *p*-values from the *t*-tests of the four variables depicted in Fig. 1 for a composite test of the fragmentation effect on the study dispersal process (p. 779, Sokal and Rohlf, 1981).

We represented the age structure of mistletoes in each habitat unit grouping observations in 2-yr classes. We compared the frequency distribution of individual ages between mistletoe populations in the fragmented and non-fragmented habitat unit of each site by means of a Kolmogorov–Smirnov test (Zar, 1984).

We summarized our main results using regression analysis where each of the six habitat units (i.e., three fragmented and three continuous) was considered as a replicate. Because disperser abundance should have an overriding influence on mistletoe seed dispersal and establishment, we related the variables we hypothesized to depict the dispersal process; i.e., number of marsupials vs. no. fruits removed and no. seeds dispersed, no. fruits removed vs. no. seeds dispersed, and no. seeds dispersed vs. no. seedlings established. Number of fruits removed, seeds dispersed, and seedlings established were expressed as a percent of fruit (=seed) production.

3. Results

The estimated minimum number of marsupials present at each sampling habitat unit ranged between 0 and 29 individuals. We found a consistent effect of forest fragmentation on the abundance of *D. gliroides*. In all three sites, the estimated number of dispersers was lower in the fragmented habitat unit than in the nearby continuous forest ($t = 1.79$, $p = 0.11$; Fig. 1a). We did not capture any *D. gliroides* in the fragmented habitat at Campanario. Large differences also occurred among the three continuous forest units. For instance, marsupial abundance in the continuous forest at Campanario was as low as in the fragmented forest at either Tacul or Llao-Llao (Fig. 1a).

The abundance of reproductive mistletoes was relatively higher in the continuous than in the nearby fragmented habitat. Along the transects set in the continuous and fragmented habitat units, we found, respectively, 25 and 19 reproductive mistletoes at Campanario; 46 and 18 at Tacul; and 43 and 23 at Llao-Llao ($t = 2.80$, $p = 0.11$). However, the number of fruits produced per mistletoe showed a more equivocal trend. The mean ± 1 SE number of fruits produced per reproductive plant was 891.2 ± 33.4 (continuous) and 736.7 ± 37.8 (fragmented) at Campanario, 641.9 ± 42.5 and 1264.4 ± 89.6 at Tacul, and 409.8 ± 12.6 and 740.9 ± 45.7 at Llao-Llao ($t = -1.17$, $p = 0.36$). Thus, mean total fruit production per transect for the fragmented and continuous habitat types were 23,143 vs. 17,933, respectively ($t = 2.21$, $p = 0.16$). Additionally, we found 59 (continuous) and 65 (fragmented) host plants among the 100 shrubs sampled in each of the two habitat units at Campanario, 97 and 55 at Tacul, and 90 and 72 at Llao-Llao. Therefore, the mean number of reproductive mistletoes per host plant was higher in the continuous than in the fragmented forest (0.46 vs. 0.31 mistletoes/host; $t = 18.67$, $p < 0.005$).

The percent of tagged fruits removed over the 10-wk sampling period ranged between 30.2% and 86.8%; with the fragmented forest at Campanario showing the lowest rate of fruit removal and the continuous forest at Llao-Llao the highest rate. Fruit removal was consistently higher in the continuous forest than in the fragmented forest unit at all three sites ($t = 3.68$, $p = 0.03$; Fig. 1b).

The estimated percentage of all seeds (=fruits) produced that were dispersed successfully ranged between 0% and 6.2%. We found no seeds dispersed in the fragmented forest at Campanario, whereas the largest percentage of seeds dispersed was recorded in the continuous forest at Llao-Llao. The percentage of seeds dispersed was consistently larger in continuous forest than in the nearby fragmented habitat unit at all three sites ($t = 1.98$, $p = 0.09$; Fig. 1c).

The number of one-year seedlings per host plant was consistently higher at the continuous than at the fragmented habitat unit in both 2000 (9 vs. 0 for Campanario; 24 vs. 0 for Tacul; 66 vs. 2 for Llao-Llao; $t = 1.99$, $p = 0.09$) and 2001 (4 vs. 0 for Campanario; 33 vs. 0 for Tacul; 72 vs. 3 for Llao-Llao; $t = 1.88$, $p = 0.10$). A similar trend was observed when the numbers of seedlings established in 2001 were expressed as a percent of the seeds produced during the previous summer ($t = 2.00$, $p = 0.09$; Fig. 1d). Although this difference was weaker for Campanario than the other two sites, we were unable to find any seedlings in the fragmented forest at that site.

We estimated that about 5% of the dispersed seeds germinated, infected the host and established a seedling in the continuous forest at Campanario. This figure could not be estimated for the fragmented forest at this site because of a lack of seeds dispersed there. Similarly, values were 7.8% (continuous) vs. 0% (fragmented) for Tacul, and 6.7% vs. 3.5% for Llao-Llao.

Overall, we found a consistent disruptive fragmentation effect on the mistletoe–marsupial dispersal interaction. Combining p-values from individual t-tests for each of the four variables depicted in Fig. 1 resulted in a highly significant composite effect ($X^2 = 20.75$, df = 8, $p < 0.01$).

Estimated mistletoe ages ranged between 2 and 16 years old. Age distributions of mistletoe populations in continuous and fragmented forest were different ($K–S = 0.242$, $p < 0.005$ for Campanario; $K–S = 0.233$, $p < 0.03$ for Tacul; and $K–S = 0.287$, $p < 0.001$ for Llao-Llao). At all three sites, mistletoe populations in continuous forest had a large proportion of young individuals (<6 years old) and were slightly j-shaped. In contrast, populations in the fragmented forests exhibited a deficiency of new recruits and the most populous age classes were either 6–7 or 8–9 year old. Very young mistletoes were absent at both Campanario and Tacul (Fig. 2).

Regression analysis showed that the abundance of *D. gliroides* was a good and significant predictor of fruit removal (Fig. 3a), whereas fruit removal was a good predictor of seed dispersal (Fig. 3b). Most notably, the abundance of *D. gliroides* closely predicts the number of seeds dispersed (Fig. 3c), and the number of seeds dispersed the number of seedlings established (Fig. 3d) after accounting for differences in seed production.

4. Discussion

Our results suggest that the negative impacts of forest fragmentation on the abundance of a marsupial seed disperser can have a strong impact on the dynamics of seeds and seedlings, with potential effects on the overall demography of mistletoe populations. Declines in the number of individuals of the seed disperser, *D. gliroides*, related closely to declines in the removal of fruits and dispersal of seeds of the mistletoe *T. corymbosus*. The number of seeds dispersed linked directly to the number of seedlings established and new recruits in the study mistletoe populations. Our results imply that the local extinction of the marsupial may completely disrupt this plant-disperser mutualism dooming mistletoe populations to extinction with unknown, but presumed widespread community-level consequences.

Effects of forest fragmentation and alteration on populations of *D. gliroides* may involve multiple and compounding direct and indirect factors. First, this highly endemic marsupial is mostly arboreal, dwelling in cavities high in the canopy of old-growth *Nothofagus* forests. Thus, one direct cause of the decline of *D. gliroides* in fragmented forests can be a reduction in the absolute amount and average patch size of its favored habitat. This could be the case of the fragmented habitat at Llao-Llao where well-defined small forest patches remain relatively isolated in the middle of a golf course in what was previously continuous forest. Second, diverse indirect effects can permeate through the borders of the remnant forest patches (Murcia, 1995), including an increase in predation (Andren and Angelstam, 1998; Nupp and Swihart, 1998) by native and introduced vertebrates, particularly domestic cats (Ebenhard, 1988; Crooks and Soule, 1999). This might be the case of the fragmented habitat at Campanario, where forest remnants are surrounded by a suburban matrix of gardens and plant nurseries.

In addition, distances as short as 50–100 m across an inhospitable habitat can represent powerful barriers that cannot be traversed by many small forest mammals (Bierregaard et al., 1992). This seems to be the case of *D. gliroides*. This marsupial was almost absent in some of the study fragments despite the high abundance of mistletoe fruits there and proximity (<100 m) of these fragments to continuous forest. This hypothesized reduction in the dispersal of *D. gliroides* due to habitat fragmentation could difficult the "rescue" of the small marsupial populations that might be trapped in
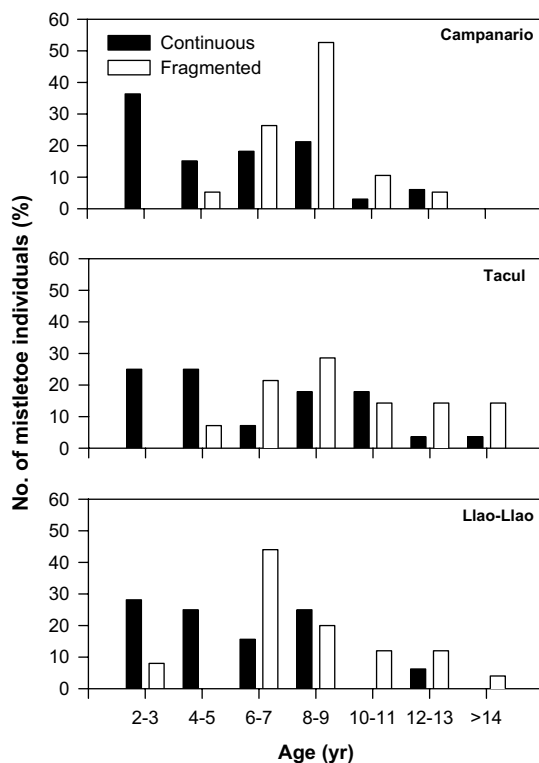

Fig. 2 – Age structure of *T. corymbosus* populations occurring in continuous vs. fragmented forest at Campanario, Tacul, and Llao-Llao.

a $r^2 = 0.75$, $p < 0.01$

% fruits removed vs No. *D. gliroides* — Continuos (●), Fragmented (○)

b $r^2 = 0.71$, $p < 0.02$

% seeds dispersed vs % fruits removed

c $r^2 = 0.98$, $p < 0.001$

% seeds dispersed vs No. *D. gliroides*

d $r^2 = 0.99$, $p < 0.001$

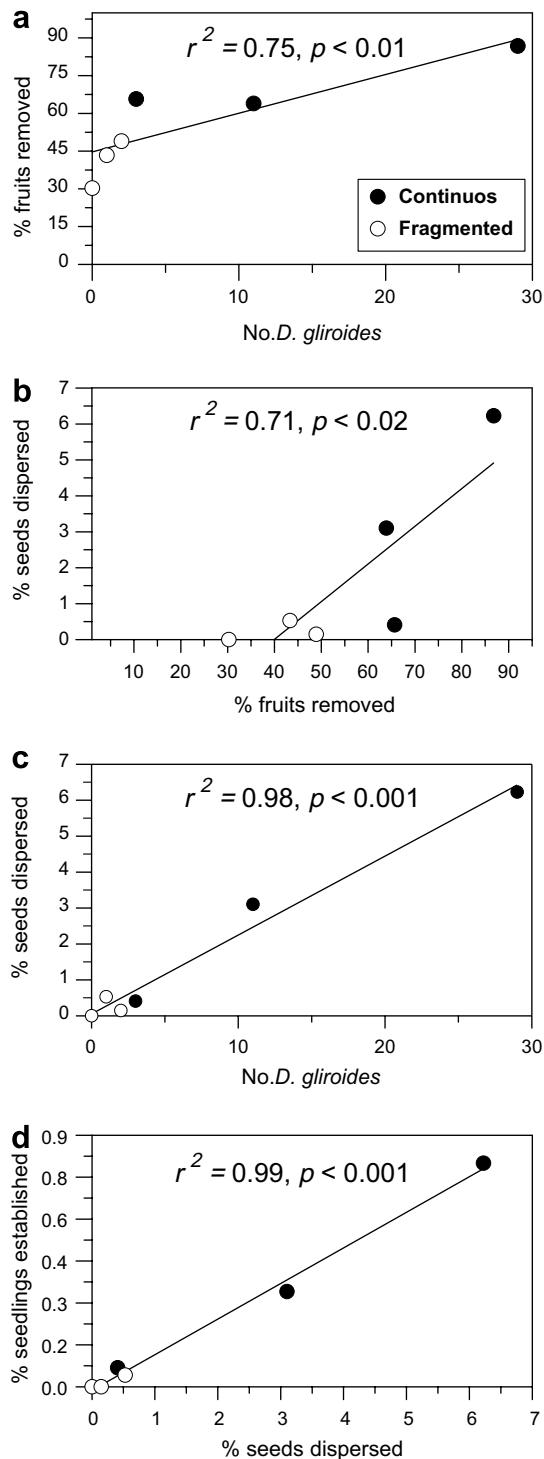% seedlings established vs % seeds dispersed

Fig. 3 – Regressions of the number (a) of individuals of *Dromiciops gliroides* vs. fruits removed, (b) fruits removed vs. seeds dispersed, (c) number of individuals of *Dromiciops gliroides* vs. seeds dispersed, and (d) seeds dispersed vs. seedlings established considering each habitat unit as a replicate. Plant variables are expressed as a percent of the fruits produced (see Section 2).

fragments, increasing the chance of their collapse due to either demographic or genetic bottlenecks (see Brown and Kodric-Brown, 1977).

Forest fragmentation affected negatively mistletoe fruit removal and seed dispersal. Although, *D. gliroides* is the sole seed disperser of *T. corymbosus* at least in the temperate forest of South America (Amico and Aizen, 2000; Aizen, 2003), mistletoe fruits are also predated by a few species of birds (e.g., *Phrygilus patagonicus*) and mice (e.g., *Oligoryzomys longicaudatus* and *Abrotrix olivaceus*). The presence of non-dispersing frugivores could explain the removal of mistletoe fruits in the fragmented forest habitat at Campanario, where we did not capture marsupials. However, although some of these animals are very opportunistic (e.g., *P. patagonicus* and *O. longicaudatus*) and might increase their presence in disturbed habitats, the abundance of *D. gliroides* seems to exert an overriding influence on mistletoe fruit removal (Fig. 3a) and be highly predictive of seed dispersal (Fig. 3c).

Fragmentation greatly affected the establishment of mistletoe seedlings. Number of seedlings declined strongly in the fragmented forest units and these effects were highly consistent across two seedling cohorts. Because mistletoe seed germination and seedling establishment are particularly susceptible to desiccation (Sargent, 1995; Yan and Reid, 1995), increased mortality due to water stress in the more light-exposed fragmented forest environment could be a plausible explanation for the patterns we found (Harrison and Bruna, 1999; Bruna, 2002). The potential for this contributing factor is partially supported by our results, i.e., a trend towards a decrease in the number of seedlings established per dispersed seed in at least two of the fragmented habitat units. However, seed dispersal seems to be the overriding factor limiting the number of established seedlings in *T. corymbosus* (Fig. 3d). Two synergetic effects reinforce this relationship: (1) the highly specific dispersal process itself that involves the defecation and "gluing" of seeds onto branches of an appropriate host plant, and (2) the passage through the marsupial guts that is critical for triggering seed germination (Amico and Aizen, 2000).

The dispersal link has been perceived as particularly critical and vulnerable in mistletoe life cycle (Reid, 1991). In our study system, the disruption of the interaction between *D. gliroides* and *T. corymbosus* may have implications not only for seedling establishment, but also mistletoe population dynamics. A decline in juveniles in all three fragmented populations and a lack of new recruits in two of these populations imply that altered patterns in seed dispersal can have important demographical consequences. In addition, we observed a decline in the abundance of reproductive mistletoes, not explained by host availability, which in turn could promote further declines of marsupial populations in forest remnants. Thus, we forecast that fragmentation of these southern forests could not only involve the local extinction of *D. gliroides*, but also of the mistletoe *T. corymbosus* through the disruption of its dispersal mutualism. This is to our knowledge one of the first fragmentation studies linking seed dispersal and plant demography. Only a few studies have focused on effects of habitat fragmentation on the plant-disperser mutualism. In Tanzania, for example, fragmentation of mountain rainforest leads to impoverished assemblages of frugivorous species, lower rates of seed dispersal, seedling establishment and juvenile recruitment of populations of several animal-dispersed tree species (Cordeiro and Howe, 2001; Cordeiro and

Howe, 2003). In other systems, plant populations in fragmented habitats can be skewed towards smaller size classes. This is the case of the clonal herb *Heliconia acuminate* in Amazonian forest fragments (Bruna and Kress, 2002). However, new recruits in *H. acuminata* can occur not only through sexual production, but also vegetative reproduction that could be fostered in forest fragments (Bruna and Kress, 2002).

The disruption of the mutualism between *T. corymbosus* and its marsupial disperser may have far-reaching consequences at the community and ecosystem levels. Because of their prolonged flowering and fruiting seasons and production of sugar-rich nectar and protein-rich fruits, mistletoes may represent critical resources during periods of food scarcity. Also, they may constitute an important cause of host mortality regulating understory plant community diversity and different ecosystem processes. Thus, many species of mistletoe, including *T. corymbosus*, can be considered keystone species in the ecosystems where they occur (Reid et al., 1995; Watson, 2001). *T. corymbosus* represents the sole winter nectar resource for the hummingbird *Sephanoides sephaniodes*—a key pollinator in the temperate forest of southern South America—over much of its geographical range (Aizen et al., 2002). Also infected hosts, most notably of the dominant understory shrub *Aristotelia chilensis*, showed symptoms of decline and increased mortality (M.A. Aizen, pers. obs.). Thus, the disruption of this mistletoe–marsupial dispersal interaction due to habitat fragmentation and other human-driven disturbances may have indirect cascading effects throughout different interaction webs.

Acknowledgements

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