

## Influence of habitat factors on the distribution and abundance of a marsupial seed disperser

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Understanding factors that influence the distribution and abundance of seed dispersers is important because of the role these species play in maintaining plant communities. The temperate forest of Patagonia has an unusually high frequency of mutualisms, including obligate seed dispersal of a keystone mistletoe (*Tristerix corymbosus*) by the marsupial *Dromiciops gliroides*. We examined whether the distribution and abundance of *D. gliroides* was related to the distribution and abundance of this mistletoe, which is a principal food source, or alternatively, whether other habitat features constrain the distribution and abundance of this marsupial. We conducted field surveys for *D. gliroides*, mistletoe, and other habitat variables and developed a set of habitat models in which model variables were defined a priori. We found that the distribution of *D. gliroides* was related to bamboo cover. Bamboo is an important source of nest material and nest sites. However, when the minimum requirement for bamboo cover was met, abundance of *D. gliroides* tracked abundance and fruit production of mistletoe plants. Habitat constraints imposed by bamboo on *D. gliroides* have important conservation implications because both anthropogenic and natural processes have significant impacts on bamboo in the temperate forest of Patagonia.

Key words: *Dromiciops gliroides*, habitat constraints, mutualisms, Patagonia, seed dispersal, *Tristerix corymbosus*

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Seed dispersers, such as frugivorous mammals and birds, play an important role in creating and sustaining diversity in plant communities (Schupp et al. 2002). Understanding the suite of factors that are needed to maintain plant–seed disperser interactions is therefore important for advancing understanding of mutualisms and for biodiversity conservation. At large scales appropriate habitat can be the most important factor limiting distribution and abundance of frugivores, including characteristics such as availability of nest sites, a diversity of food resources, and distance between food and shelter (Fedriani 2005; Wiens 1989). At small scales characteristics of the habitat surrounding fruiting plants also can be important because frugivores might select plants or good patches based on habitat features rather than on plant phenotypic traits (Fedriani 2005; Herrera 1998). For example, frugivores could minimize predation risk by selecting sites with high vegetative cover to avoid predators during foraging (Howe 1979). The distribution and abundance of species also depend, in part, on the distribution and abundance of other species with which they interact (Wiens 1989). However, the

majority of plants that depend on frugivorous animals for seed dispersal are dispersed by several species of animals, and most animal dispersers consume fruit of several plant species (Herrera 1998, 2002). Thus, specific pairwise interactions between a plant and a given frugivore are generally weak (Bascompte et al. 2006; Vazquez et al. 2007), and habitat factors can limit the degree to which distribution or dynamics of frugivorous animals correlate with a particular food resource.

In contrast to the weak mutual dependence of most plants and their seed dispersers, some mutualisms in the temperate forest of Patagonia in southern South America appear to be obligate, and a large proportion of the flora depends on mutualistic animals (Aizen and Ezcurra 1998; Aizen et al. 2002; Armesto et al. 1996). This level of mutualism is one of the highest recorded for temperate ecosystems and is



comparable to levels from tropical forests (Willson 1991; Willson et al. 1989). Unlike the mutualism structure in tropical forests, in this temperate forest many species of flora depend on a few mutualistic animals (Aizen et al. 2002). The northern portion of the temperate forest harbors a unique triangle of keystone mutualists comprised of a hummingbird (picaflor rubi or green-backed fire crown [*Sephanoides sephanioides*]), a mistletoe (quintral [*Tristerix corymbosus*]), and a marsupial (monito del monte [*Dromiciops gliroides*])—Amico and Aizen 2000), which is the only living representative of Microbiotheriidae, one of the oldest lineages of marsupials (Marshall 1978). The hummingbird is responsible for pollinating nearly 20% of the endemic species of woody flora in this biome (Aizen et al. 2002; Armesto et al. 1996). The mistletoe blooms in winter and is the only source of nectar for the hummingbird during that period (Aizen and Ezcurra 1998; Smith-Ramírez 1993). *D. gliroides* is the only known disperser of the mistletoe in this forest, and passage of the seed through the gut of *D. gliroides* is crucial to triggering germination (Amico and Aizen 2000). Other research suggests that *D. gliroides* also disperses seeds of 80% of the flora with fleshy fruits in this forest (Amico and Aizen 2000; Amico et al. 2009). Understanding factors that influence the distribution and abundance of these keystone species is important for conserving these species and the roles they play in maintaining the temperate forest of Patagonia. In this study we focus on *D. gliroides*.

We conducted field surveys for *D. gliroides*, mistletoe, and other habitat variables and developed a set of habitat models in which model variables were defined a priori to test the hypothesis that the distribution and abundance of *D. gliroides* are related to the distribution and abundance of mistletoe, or alternatively, to habitat structure of other food plants, or both. We hypothesized that the distribution and abundance of *D. gliroides* might be related to the abundance of mistletoe because *D. gliroides* influences recruitment of the mistletoe (García et al. 2009; Rodríguez-Cabal et al. 2007), and mistletoe serves as a high-density resource patch for *D. gliroides*. Alternatively, because of the diversity of fruits available at our site, the distribution and abundance of *D. gliroides* might be constrained largely by habitat features such as vegetative cover and structural complexity of the habitat that influence nest site availability, predation risk, and other aspects of their biology. Other habitat studies have shown that this species uses a variety of forest types (Fontúrbel et al. 2010; Smith-Ramírez et al. 2010) and that abundances of *D. gliroides* and mistletoe are associated in some areas (García et al. 2009) but not others (Smith-Ramírez et al. 2010).

## MATERIALS AND METHODS

**Study area.**—We conducted our research in Nahuel Huapi National Park (41°01'S, 71°30'W, 705,000 ha) and an adjacent reserve, Llao-Llao Municipal Reserve (41°08'S, 71°19'W, 1,226 ha), in northwestern Patagonia, Argentina. Native forest vegetation in the study area belongs to the Subantarctic biogeographical region (Cabrera 1976). The most

common trees are evergreen southern beech (*Nothofagus dombeyi*), deciduous lenga beech (*Nothofagus pumilio*), and a conifer (*Austrocedrus chilensis*). Understory is dominated by bamboo (*Chusquea culeou*) and the shrub *Aristotelia chilensis*, which is the main host of mistletoe in the study area (Mermoz and Martín 1986). Two forest layers are well differentiated, with tree canopy reaching a height of 40 m and understory reaching to 5 m. Nearly 50% of the woody species in the understory of the study have fleshy fruits (Amico and Aizen 2005). Cattle roam freely through large parts of Nahuel Huapi National Park but have been excluded from Llao-Llao Municipal Reserve for several decades. Mean January temperature is 15°C, and mean July temperature is 3°C (Mermoz and Martín 1986).

**Sampling design.**—We conducted presence–absence surveys of *D. gliroides* and examined habitat variables at 17 plots (each 50 × 50 m) in Nahuel Huapi National Park. In addition, trapping was conducted at 12 plots (each 50 × 50 m) in Llao-Llao Municipal Reserve to determine the relationship between abundance of *D. gliroides* and abundance of mistletoe and other habitat variables. Plots at Nahuel Huapi National Park and Llao-Llao Municipal Reserve were located in continuous forest. Plots were separated from each other by at least 5 km (maximum distance 50 km) for the plots in the presence–absence surveys and by 500 m (maximum distance 2 km) for the plots in the abundance surveys. Plots in Nahuel Huapi National Park were chosen randomly to incorporate the range of forest conditions found in the study area. Potential plots in Llao-Llao Municipal Reserve were stratified by mistletoe density, and 4 plots were chosen randomly within each of the following categories: high (>35 reproductive individuals of mistletoe per hectare), low (<20 reproductive individuals per hectare), and no mistletoe. Plots were stratified on abundance of mistletoe because mistletoe has a patchy distribution and a range of other variables can be found within each stratum defined by mistletoe density. We conducted most fieldwork during the austral summer (December 2006–March 2007) because *D. gliroides* hibernates during winter and the main fruiting and dispersal season of the mistletoe is summer (Aizen 2003).

**Presence–absence of *D. gliroides*.**—To facilitate rapid surveys of presence–absence of *D. gliroides* the 17 study plots throughout Nahuel Huapi National Park were grouped by presence or absence of mistletoe. At plots with mistletoe we examined all plants < 15 cm in diameter at breast height in each plot for dispersed mistletoe seeds. When *D. gliroides* defecates mistletoe seeds, the sticky pulp that surrounds the seeds facilitates attachment to the branch resulting in “necklaces” of up to 20 seeds linked by viscin threads. We concluded that *D. gliroides* was present if we found mistletoe seeds dispersed. If no dispersed seeds were found in the plot, we used trapping to determine the presence of *D. gliroides*. Trapping also was conducted in plots with no mistletoe. Within each plot we placed a 5 × 5 grid of Tomahawk-style traps (15 × 15 × 25 cm) about 10 m apart. Previous trapping in our study area indicated that this grid size was large enough to

**TABLE 1.**—Means ( $\pm$  SDs) of habitat variables and summary ANOVA for comparison of means for plots in Nahuel Huapi National Park in northwestern Patagonia, Argentina, where *Dromiciops gliroides* was present or absent. Means ( $\pm$  SDs) of raw data are shown. See “Materials and Methods” for details on habitat variables.

Habitat variables	Mean $\pm$ SD		$F_{1,15}$	$P$
	Present ( $n = 9$ )	Absent ( $n = 8$ )		
No. reproductive mistletoe <sup>a</sup>	1.17 $\pm$ 1.49	1.48 $\pm$ 1.69	0.06	0.81
Crop size of mistletoe <sup>a</sup>	429.26 $\pm$ 479.62	643.96 $\pm$ 1,049.16	0.20	0.66
No. <i>Aristotelia chilensis</i> plants <sup>a</sup>	2.91 $\pm$ 3.50	1.23 $\pm$ 1.73	1.50	0.23
Crop size of <i>A. chilensis</i> <sup>a</sup>	55.35 $\pm$ 64.38	61.06 $\pm$ 172.70	2.26	0.15
No. <i>Azara microphylla</i> plants	0.07 $\pm$ 0.21	0.25 $\pm$ 0.71	0.55	0.47
Bamboo cover (%) <sup>a</sup>	16.24 $\pm$ 18.23	0.44 $\pm$ 1.08	8.95	<0.001
Habitat complexity	3.18 $\pm$ 0.87	3.01 $\pm$ 1.05	0.35	0.73
Canopy cover (%) <sup>a</sup>	54.70 $\pm$ 20.60	46.28 $\pm$ 35.79	2.87	0.10
Average diameter at breast height	53.13 $\pm$ 24.59	21.00 $\pm$ 39.59	3.80	0.08

<sup>a</sup> Variables were log-transformed prior to analysis.

obtain a sufficient sample of individuals (Rodríguez-Cabal et al. 2007, 2008), although more recent studies with radiotelemetry have shown home ranges of 1.3 ha in Llao-Llao Municipal Reserve (Rivarola 2009) and home ranges of 1.6 ha  $\pm$  0.6 SD in fragmented forests in Chile for this species (Fontúrbel et al. 2010; Franco et al. 2011). Each trap was placed between 1 and 2 m above ground in the shrub closest to the sample point. Traps were baited with apple and banana. Because the objective was to document presence, once a *D. gliroides* was trapped we stopped trapping at the plot (except in plots where we determined abundance; see below). Sampling for presence-absence was continued for 4 nights if no *D. gliroides* was captured. Based on previous capture data for *D. gliroides* (Rodríguez-Cabal et al. 2007, 2008), and following procedures in MacKenzie et al. (2002), probability of capture was 99.6% in 4 nights if *D. gliroides* was present. We concluded that *D. gliroides* was absent after 4 nights of trapping if no *D. gliroides* was captured.

**Abundance of *D. gliroides*.**—We estimated abundance of *D. gliroides* using multiple capture-recapture methods with trapping grids as described above. This measure of abundance represents an estimate of the number of animals that exhibit at least some of their activity in the plot, not the number of animals that maintain home ranges within the plot. At each of the 12 plots in Llao-Llao Municipal Reserve animals were trapped for 4 periods of 4 nights each. Traps were checked daily, and all *D. gliroides* captured were marked with an individual code using ear clips and released at the point of capture (Rodríguez-Cabal et al. 2007). Recaptures were noted in subsequent trapping periods. We report the total number of unique individuals captured for all plots to allow for comparison among plots (Wilson et al. 1996). The low number of captures in plots without mistletoe precluded use of other methods to estimate abundance. Research on live animals conformed to guidelines of the American Society of Mammalogists (Sikes et al. 2011) and was approved by the University of Florida Animal Care and Use Committee.

**Habitat variables.**—At each of the 17 plots in Nahuel Huapi National Park a 5  $\times$  5 grid was established with points 10 m apart. We measured a suite of habitat variables in 5-m-radius circular subplots centered on every 2nd point ( $n = 13$  per

plot). Similar sampling was conducted at plots trapped in Llao-Llao Municipal Reserve, with subplots centered on every 2nd trap. We measured the following variables to represent the biological and physical structure of the habitat: number of reproductive individuals and crop size of the 3 most common understory plants consumed and dispersed by *D. gliroides* (mistletoe, *A. chilensis*, and *Azara microphylla*—Amico et al. 2009), cover and height of bamboo, complexity of habitat structure, canopy cover, understory cover, and diameter at breast height of all trees. In addition, for mistletoe we counted the number of nonreproductive individuals (2–4 years old), seedlings (those presenting the first 2 true leaves), and number of seeds dispersed. To determine crop size of understory plants we counted the number of fruits on a subset of 3 branches dispersed in each crown and then estimated total crop size by multiplying mean number of fruits per branch by total number of branches in the crown for each plant. Cover of bamboo was estimated visually by summing the total area occupied by bamboo stems and leaves in each subplot. Also, we measured height of the tallest bamboo stem in each subplot. As a measure of habitat complexity within each subplot, we counted the number of contacts with a vertical pole (3-m height) for branches 5–10 cm in diameter and oriented  $\leq 45^\circ$  relative to the ground. Good connectivity between plants in the understory stratum could play a key role in the mobility of this animal, and more seeds dispersed in feces of *D. gliroides* are found on branches with these characteristics (Amico 2000). Percent cover of the canopy and understory were estimated using a densiometer at the center of the circular subplot.

**Statistical analysis.**—We used analysis of variance (ANOVA) to compare habitat variables among plots where we recorded presence versus absence of *D. gliroides*. We used multiple logistic regression to determine which habitat variables predicted presence of *D. gliroides* throughout Nahuel Huapi National Park. In addition, we used multiple regression to assess the contribution of habitat variables to explaining abundance of *D. gliroides* in Llao-Llao Municipal Reserve. A Shapiro-Wilk  $W$ -test was used to test normality. Data were log-transformed when necessary to achieve normality and reduce heteroscedasticity (Table 1). For both analyses we used only explanatory variables that did not correlate significantly with

**TABLE 2.**—Summary of the competitive logistic regression models ( $\Delta AIC < 2$ ) constructed to determine which habitat variables predicted presence–absence of *Dromiciops gliroides* at the 17 study plots in Nahuel Huapi National Park in northwestern Patagonia, Argentina. Significant variables in each model are indicated by an asterisk (\*). See “Materials and Methods” for details on habitat variables.  $AIC_c$  = small-sample version of Akaike’s information criteria;  $\Delta AIC$  = difference between the  $AIC_c$  score for each model and the  $AIC_c$  score of the best model.

Models	Habitat variables	$AIC_c$	$\Delta AIC$	$r^2$	$\beta$	Predicted correct (%)	
						Absent	Present
Fruit abundance and bamboo		0.82	0	0.61		88.9	88.9
	Crop size of mistletoe						
	Crop size of <i>Aristotelia chilensis</i>						
Bamboo	Bamboo cover*	1.12	0.31	0.37	29.04	77.8	66.7
	Bamboo cover*						

one another after a Bonferroni correction. Two sets of variables were correlated for plots where we measured presence–absence and abundance. We omitted bamboo height and understory cover because these measures were correlated with bamboo cover and habitat complexity, respectively, and bamboo cover and habitat complexity might be related more directly to the biology of *D. gliroides*, particularly for nest material and mobility. We did not include crop size of *A. microphylla* in analyses because this understory plant did not fruit during the study year.

Seven models were built to identify habitat variables related to the presence–absence and abundance of *D. gliroides*. Rather than examine all possible models, models were developed based on a priori hypotheses that focused on mistletoe, other food plants, and habitat structure as key factors in the distribution and abundance of *D. gliroides*. We examined the following models: global—all habitat variables; food plants—number of reproductive individuals of major food plants that produce fleshy fruits eaten by *D. gliroides*; fruit abundance and bamboo—crop size of plants with fleshy fruits and cover of bamboo; mistletoe plants and bamboo—number of reproductive mistletoes and bamboo cover; mistletoe plants; bamboo; and habitat structure—all habitat variables unrelated to food plants.

We used Akaike’s information criteria (AIC), which allow direct comparison of models with different numbers of parameters. The best-fitting model has the smallest AIC (Burnham and Anderson 2002; Whittingham et al. 2005). We applied the small-sample version of AIC ( $AIC_c$ ) because the ratio of number of observations to number of parameters was  $< 40$ .  $\Delta AIC$  represents the difference between the  $AIC_c$  score for each model and the  $AIC_c$  score of the best model. Models with  $\Delta AIC$  values  $< 2$  are competitive (Burnham and Anderson 2002).

To evaluate goodness-of-fit for multiple logistic regression models we used Nagelkerke  $r^2$ , which is based on comparison of the likelihood of the current model to the null model (i.e., one without predictors—Hosmer and Lemeshow 1989). We evaluated the importance of significant independent variables in logistic regression using the standardized regression coefficient  $\beta$ , which is the predicted change in odds for a unit increase in the corresponding independent variable (Hosmer and Lemeshow 1989). In multiple regressions we

evaluated the importance of significant independent variables by calculating the standardized regression coefficient  $\beta$  (Ganas and Robbins 2005). Finally, we performed simple regression analyses to examine the relationship between abundance of *D. gliroides* and habitat variables that occurred in the competitive multiple and logistic regression models. Analyses were conducted using SAS 9.13 and JMP IN for Windows version 5.1 (SAS Institute Inc., Cary, North Carolina). The criterion for statistical significance was  $P < 0.05$ .

## RESULTS

*Presence–absence of D. gliroides.*—*Dromiciops gliroides* was present at 9 of 17 survey plots. These plots had more bamboo cover than plots without *D. gliroides*, and no other variables differed significantly between plots where *D. gliroides* was present versus absent (Table 1). *D. gliroides* was present at 3 plots with no mistletoe, and mistletoe was present at 4 plots where *D. gliroides* was absent. However, in all plots without *D. gliroides* we did not find mistletoe seeds dispersed, seedlings, or nonreproductive mistletoe (2–4 years old), indicating that no mistletoe recruitment had occurred in at least the last 4 years. Two of the 7 multiple logistic regression models were competitive for explaining presence–absence of *D. gliroides* (Table 2). The most parsimonious model (fruit abundance and bamboo) explained almost 90% of the variation in presence–absence of *D. gliroides*. Bamboo cover was the only significant predictor variable in the top models. *D. gliroides* was recorded in 100% of the plots that had  $> 10\%$  bamboo cover and in only 33% of the plots with  $< 10\%$  cover.

*Abundance of D. gliroides.*—*Dromiciops gliroides* was captured in the first 4 nights of trapping at 10 of the 12 plots, but local abundance varied substantially among plots (Fig. 1). Within a plot the number of captures of different individuals ranged from 0 to 45, and the number of individuals recaptured at least once ranged from 0 to 24. The 2 plots where no animals were captured were the only plots with  $< 10\%$  bamboo cover. These plots, and 2 additional plots where *D. gliroides* was recorded, also had no mistletoe. The most parsimonious model for abundance of *D. gliroides* contained only the number of reproductive mistletoe plants (Table 3), with mistletoe explaining 80% of the variation. Abundance of

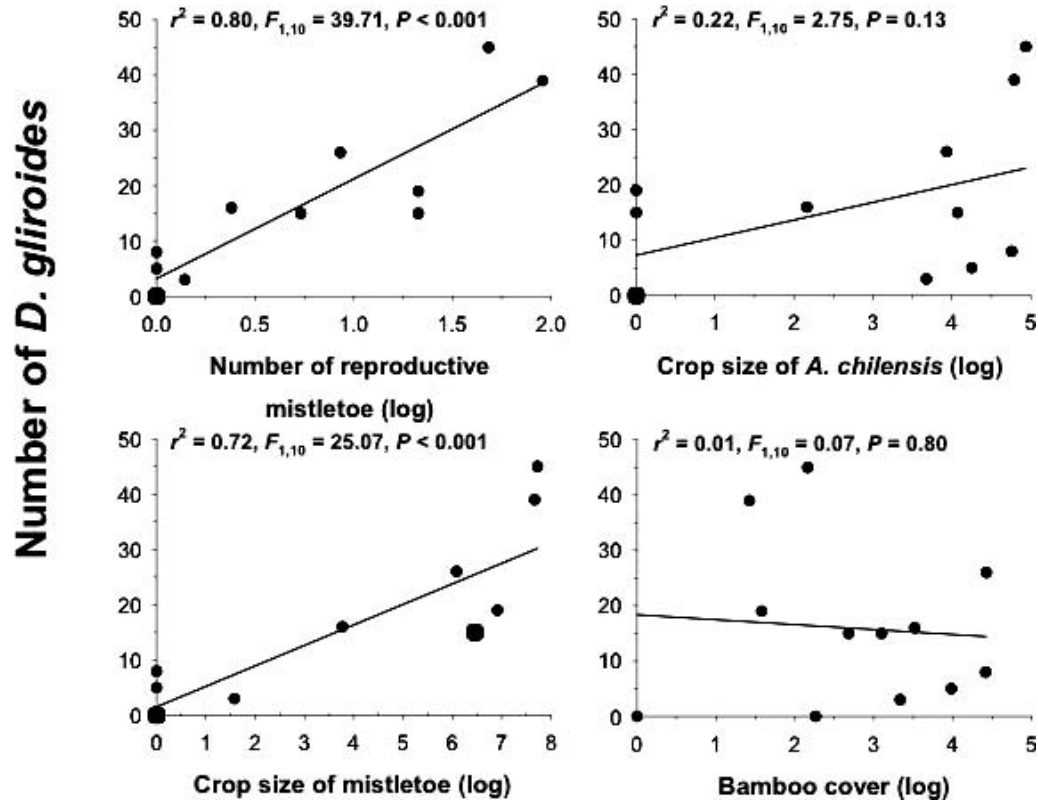


FIG. 1.—Simple linear regression of the number of *Dromiciops gliroides* on predictor variables of the competitive logistic and multiple regression models for sample plots in Llao-Llao Municipal Reserve in northwestern Patagonia, Argentina. Coefficients of determination ( $r^2$ ) and  $P$ -values are shown. Larger dots represent more than 1 data point.

*D. gliroides* increased as the number of reproductive mistletoe plants or crop size of mistletoe increased (Fig. 1). Bamboo cover and abundance of *D. gliroides* were not related (Fig. 1). Similarly, crop size of *A. chilensis* and other habitat variables explained little variation in the abundance of *D. gliroides* (Fig. 1).

### DISCUSSION

Based on our sampling throughout Nahuel Huapi National Park, structural habitat features strongly influenced the distribution of *D. gliroides*, and mistletoe and other food plants were not significant predictors of the presence of *D. gliroides*. Four plots with mistletoe did not have *D. gliroides*. If this is the only seed disperser of mistletoe in this temperate forest, as concluded from previous studies (Amico and Aizen

2000), presumably *D. gliroides* was present in the area when mistletoe plants were established in these plots. The absence of seedlings and nonreproductive mistletoe (2- to 4-year age class) in plots where we did not detect *D. gliroides* is consistent with local extirpation of *D. gliroides*, but other factors also could influence recruitment of mistletoe.

Bamboo cover was the most important habitat feature explaining presence-absence of *D. gliroides*. Leaves of bamboo are a principal resource for nest building for *D. gliroides*, and because *D. gliroides* is arboreal, bamboo can increase mobility of this species in forest understory where food and nests are located and provide cover from predators (Jimenez and Rageot 1979; Mann 1955). In contrast, surveys conducted at Llao-Llao Municipal Reserve did not show a significant association between abundance of *D. gliroides* and cover of bamboo, although *D. gliroides* was absent from the 2

TABLE 3.—Summary of the competitive regression models ( $\Delta AIC < 2$ ) constructed to determine which habitat variables predicted abundances of *Dromiciops gliroides* at 12 study plots in Llao-Llao Municipal Reserve in northwestern Patagonia, Argentina. Significant variables in each model are indicated by an asterisk (\*). See “Materials and Methods” for details on habitat variables.  $AIC_c$  = small-sample version of Akaike’s information criteria;  $\Delta AIC$  = difference between the  $AIC_c$  score for each model and the  $AIC_c$  score of the best model.

Models	Habitat variables	$AIC_c$	$\Delta AIC$	$r^2$	$\beta$	$P$
Mistletoe		48.47	0	0.80		
	No. reproductive mistletoe*				0.89	<0.0001
Mistletoe plants and bamboo		49.40	0.93	0.83		
	No. reproductive mistletoe*				0.95	<0.0001
	Bamboo cover					

plots with <10% of bamboo cover. The lack of importance of bamboo in explaining abundance of *D. gliroides* in the reserve could be explained if, once the minimum requirement for bamboo cover is met, other factors play a more important role than bamboo in controlling the number of *D. gliroides* the habitat can support.

*Dromiciops gliroides* was present at plots without mistletoe, indicating that the mistletoe–*D. gliroides* association is not an obligate partnership for *D. gliroides*. However, a significant association occurred at Llao-Llao Municipal Reserve between abundance of *D. gliroides* and abundance of mistletoe plants and fruits. These results are consistent with other data that show corresponding spatial patchiness in the distribution of *D. gliroides* and mistletoe along a transect in this reserve (García et al. 2009). The strong relationship between mistletoe abundance and abundance of *D. gliroides* at this reserve might occur because larger numbers of *D. gliroides* result in greater recruitment of mistletoe, populations of *D. gliroides* are responding to abundance of mistletoe fruit, or both species are responding to another related habitat variable not measured in this study. The importance of *D. gliroides* for dynamics of the mistletoe has been established (Amico and Aizen 2000; García et al. 2009; Rodríguez-Cabal et al. 2007). Experiments are needed to determine the importance of mistletoe for populations of *D. gliroides*, but several observations suggest that mistletoe could affect the dynamics of this species. Mistletoe produces a large crop size every year and is the most abundant fleshy fruit in the northern temperate forest of Patagonia (Aizen 2003). Also, mistletoe plants are aggregated, resulting in patches with predictable high densities of fruit resources. Examination of data from other sites shows that once mistletoe fruits are ripe *D. gliroides* consumes almost exclusively mistletoe (Rodríguez-Cabal et al. 2007). Some studies of other species support a positive relationship between fruit abundance and frugivore abundance (Krebs et al. 2010; Moegenburg and Levey 2003; Ortiz-Pulido and Rico-Gray 2000; Rey 1995; Saracco et al. 2005), and others suggest little or no relationship (García and Ortiz-Pulido 2004; Herrera 1998; Telleria and Perez-Tris 2007). However, the majority of studies on the relationship between fruit availability and abundance of frugivores have examined interactions between fruiting plants and frugivorous birds (Herrera 1998, 2002; Jordano 1994, 2000, Levey 1988; Loiselle and Blake 2002). Birds are highly mobile and can move among resource patches at a variety of scales in response to changes in fruit abundance. In contrast, a small mammal like *D. gliroides* that lives mainly in the understory cannot exploit widely distributed resource patches that might provide food when the local fruit crop is scarce. As a result, local resources, such as mistletoe fruit, could have stronger effects on abundance of small mammals such as *D. gliroides* than on more mobile species. Similarly, berry crops are strong predictors of temporal fluctuations in small mammal populations in boreal forests (Krebs et al. 2010).

Although considerable progress has been made in understanding plant–animal mutualisms in the Patagonian forest

(Aizen 2003; Amico and Aizen 2000; García et al. 2009), we are only in the early stages of understanding the complex interactions of these organisms with other aspects of the environment. Because of the important role of *D. gliroides* as a seed disperser in the Patagonian forest, habitat changes that affect this species could have indirect cascading effects through the rest of the community. Several anthropogenic and natural processes have significant impacts on distribution and cover of bamboo in temperate forests of Patagonia and, thus, likely have indirect impacts on *D. gliroides*. Browsing by introduced ungulates alters composition of the forest and greatly reduces bamboo understory (Raffaele et al. 2007; Veblen et al. 1992). Cattle and other introduced ungulates, such as red deer (*Cervus elaphus*) and fallow deer (*Dama dama*), occur over large parts of the Patagonian forest, including parks and reserves (Blackhall et al. 2008), and might constitute an important threat to *D. gliroides*. Natural and anthropogenic fires also might affect *D. gliroides* in the short term by removal of bamboo and in the long term by changing the composition and structure of the forest (Kitzberger and Veblen 1999). In addition, in this forest bamboo blooms and dies at approximately 40- to 60-year intervals. Although these natural die-offs are not synchronous over the entire forest, very large patches die (i.e., thousands of hectares—Kitzberger et al. 2007), temporarily creating large patches of habitat unsuitable for *D. gliroides*.

Habitat fragmentation also negatively affects abundance of *D. gliroides* (Fontúrbel et al. 2010; Rodríguez-Cabal et al. 2007; Saavedra and Simonetti 2005), and local extinctions of this species have been associated with complete disruption of mistletoe seed dispersal (Rodríguez-Cabal et al. 2007). Loss and fragmentation of Patagonian forests is relatively low in Argentina, but enormous amounts of forest have been cleared in Chile, resulting in landscapes composed of forest fragments and strips of riparian forest (Echeverría et al. 2006). The mechanisms through which habitat fragmentation affects *D. gliroides* are unknown, but the impact of processes leading to loss of bamboo can be amplified with habitat fragmentation. Effects of browsing by livestock often are particularly acute in forest fragments because livestock have easy access to the entire patch. Loss of bamboo within habitat fragments from livestock browsing or natural die-offs could have severe consequences because these patches are isolated, reducing the probability of demographic rescue and recolonization by *D. gliroides* following regeneration of bamboo within the patch. Clearly, effective long-term conservation of the Patagonian forest will need to focus not only on maintaining the elements that contribute to biodiversity and biological interactions (Vazquez and Simberloff 2003) but also on incorporating an understanding of the environmental factors that limit these interactions.

## RESUMEN

Entender los factores que influencia la distribución y abundancia de los dispersores de semillas es importante por el rol que estas especies juegan en el mantenimiento de la biodiversidad. El bosque templado de Patagonia contiene un

inusual número de mutualismos, incluyendo la dispersión de semillas de una especie clave, el muérdago (*Tristerix corymbosus*) por el marsupial *Dromiciops gliroides*. En este trabajo examinamos si la distribución y abundancia de *D. gliroides* estaba relacionada con la distribución y abundancia del muérdago, el cual es una de las fuentes principales de alimento, o alternativamente, si otras características del hábitat restringen la distribución y abundancia de este marsupial. Nosotros realizamos relevamientos de *D. gliroides*, muérdago, y otras características del hábitat y con éstas desarrollamos modelos en los cuales las variables del hábitat fueron definidas a priori. Encontramos que la distribución del *D. gliroides* esta relacionada con la cobertura de la caña. La caña es un importante recurso para la construcción de los nidos y como sitio de nidificación. Sin embargo, cuando los requisitos mínimos de caña son cubiertos, la abundancia de *D. gliroides* esta más relacionada con la abundancia y la producción de frutos del muérdago. Los límites impuestos por la caña al *D. gliroides* tienen implicancias importantes para la conservación debido a que los disturbios antropogénicos y naturales impactan significativamente sobre las poblaciones caña en los bosques templados de Patagonia.

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