

Neighborhood effects on seed dispersal by frugivores: testing theory with a mistletoe–marsupial system in Patagonia

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Abstract. The outcome of the dispersal process in zoochorous plants is largely determined by the behavior of frugivorous animals. Recent simulation studies have found that fruit removal rates and mean dispersal distances are strongly affected by fruiting plant neighborhoods. We empirically tested the effects of conspecific fruiting plant neighborhoods, crop sizes, and plant accessibility on fruit removal rates and seed dispersal distances of a mistletoe species exclusively dispersed by an arboreal marsupial in Northern Patagonia. Moreover, in this study, we overcome technical limitations in the empirical estimation of seed dispersal by using a novel ¹⁵N stable isotope enrichment technique together with Bayesian mixing models that allowed us to identify dispersed seeds from focal plants without the need of extensive genotyping. We found that, as predicted by theory, plants in denser neighborhoods had greater fruit removal and shorter mean dispersal distances than more isolated plants. Furthermore, the probability of dispersing seeds farther away decreased with neighborhood density. Larger crop sizes resulted in larger fruit removal rates and smaller probabilities of longer distance dispersal. The interplay between frugivore behavioral decisions and the spatial distribution of plants could have important consequences for plant spatial dynamics.

Key words: dispersal kernel; Dromiciops glioroides; fruit removal; Tristerix corymbosus.

INTRODUCTION

Many ecological questions related to plant population and community dynamics, biological invasions, restoration, and responses to habitat changes, require understanding the process of seed dispersal (Levin et al. 2003, Levine and Murrell 2003). Since the seeds of the majority of terrestrial woody plant species are dispersed by frugivorous animals (Herrera 2002), the outcome of the dispersal process is largely determined by the behavior of the animals handling fruits and depositing seeds (Westcott et al. 2005, Russo et al. 2006, Spiegel and Nathan 2007). At the same time, the behavior of frugivorous animals is influenced by factors such as intra- and interspecific interactions (Carlo 2005), seasonality (Wheelwright 1988, Carlo et al. 2003, Carnicer et al. 2009), and the physical structure of the landscapes they inhabit (García et al. 2011). A potentially important but often neglected consequence of seed dispersal by animals is that not all plants in a population experience the same level of fruit removal or have similar dispersal kernels (Morales and Carlo 2006, Carlo and Morales 2008). This is due to the effects of the local environment on visitation rates by frugivores and their

subsequent movement patterns (Herrera and Jordano 1981, García and Chacoff 2007, Uriarte et al. 2011).

Recent spatially explicit simulation studies provide theoretical evidence that plant neighborhoods could be important in modulating seed dispersal processes (Morales and Carlo 2006, Carlo and Morales 2008). In these simulations, plants in denser fruiting neighborhoods experience higher fruit-removal rates compared to more isolated ones (although fruit removal could saturate or even decrease at very high neighborhood densities when frugivores are limited). Another neighborhood effect is that predicted dispersal distances are shorter for plants in dense neighborhoods, while isolated plants often show longer and fatter dispersal tails. These results are explained by simple behavioral rules; simulated animals biased their movements toward plants with more fruits and, all things being equal, preferred to visit nearby plants rather than distant ones. These rules are plausible for many organisms but it is likely that other behavioral traits specific to particular dispersers could translate into inequalities in the seed dispersal process. For example, some plants may pose higher predation risks for frugivores, could be more difficult to access due to their morphology, or be far away from other important resources for the animals.

A fair number of field studies document how fruiting plant neighbors affect fruit-removal rates by creating facilitation or competition among plant neighbors that share frugivores (Manasse and Howe 1983, Sargent 1990, García et al. 2001, Carlo 2005, Saracco et al. 2005,

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Blendinger and Villegas 2011). As far as we are aware, there are no empirical studies examining how seed dispersal distances are affected by neighborhood and crop size variables, or probing on the effects of neighborhood-mediated dispersal on plant population dynamics. However, many studies of seed rain (i.e., seed deposition) indirectly document neighborhood effects on dispersal. Dispersal of zoochorous plants is contagious and patchy (Schupp et al. 2002), with both seed rain and plant recruitment usually increasing in areas where fruiting resources are more dense or diverse (Howe and Smallwood 1982, Aukema and Martínez del Río 2002, Fragoso et al. 2003, Kwit et al. 2004, Hampe et al. 2008).

Patchy seed dispersal can arise from feedbacks between the spatial distribution of fruiting plants and the behavioral responses of frugivores to these patterns, thus contributing to create and maintain spatial structure and heterogeneity in plant populations (Aukema 2004). If neighborhoods (and clumping) of zoochorous plants have generalizable effects on fruit removal and dispersal kernels, then phenomena such as plant population responses to climate and global change, invasions of introduced species, and restoration of frugivore-dispersed endangered plant species can be better modeled and managed. Thus, it is fundamental to test whether these general predictions hold for animal-plant seed dispersal systems in the field.

Here, our objective is to test theoretical predictions regarding neighborhood effects on seed dispersal. Some predictions such as differences in fruit removal rates are easy to measure in the field, but seed dispersal distance is more elusive as it requires differentiation of seeds from multiple maternal sources. For this we used a new seed-tracking technique based on the enrichment of focal plants with ^{15}N to track their seeds in sample batches across distances (Carlo et al. 2009). Specifically, we explored the effects of crop size, plant accessibility, and fruiting plant neighborhoods on fruit removal rates and seed dispersal distances of the mistletoe *Tristerix corymbosus* (Loranthaceae), a hemiparasitic plant found in northwest Patagonia, Argentina, whose seeds are apparently being exclusively and efficiently dispersed by the small arboreal marsupial Monito del Monte (*Dromiciops gliroides*; Appendix A; see also Amico et al. 2011).

STUDY SYSTEM

The study was conducted at the Llao Llao Municipal Park (41°0' S, 71°30' W), located near San Carlos de Bariloche in Argentina. Annual precipitation reaches about 1800 mm and mean temperatures are 15°C for summer and 3°C for winter. The vegetation belongs to the Subantarctic Biogeographic Region, with a canopy dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis*. The understory is dominated by small trees such as *Aristolelia chilensis*, *Azara microphylla*, *Maytenus boaria*, and the bamboo *Chusquea culeou*. The

mistletoe *T. corymbosus* produces red tubular bisexual flowers (~5 cm long) and is pollinated by the hummingbird *Sephanoides sephaniodes* (Aizen 2003). Flowers mature into pseudoberries (~0.9 × 0.6 cm), each containing one seed (~0.6 cm long) surrounded by a viscous pulp. The fruiting season is in the austral summer from mid-December to April. In our study site, the seeds are dispersed by the endemic *Dromiciops gliroides*, a small (about 10 cm long excluding its 10 cm prehensile tail) arboreal and nocturnal marsupial (Amico and Aizen 2000, Amico et al. 2011).

Selection of focal plants in neighborhoods.—Twenty focal *T. corymbosus* plants within 15.5 ha and at least 40 m from each other were chosen to represent a gradient of low to high intraspecific neighborhood densities (Appendix B: Fig. B1, first column). Intraspecific neighborhood density was measured by mapping and measuring the size (largest diameter) of all *T. corymbosus* plants found within a radius of 5 m from the focal plants. All plants were located in the lower forest strata at a height of 0–3 m, which is where the most common host trees (*Aristolelia chilensis* and *Maytenus boaria*) are found (García et al. 2009).

Physical connectivity and accessibility of focal plants.—Based on our direct observations of *D. gliroides* movement after release during mark recapture studies and on video footing using camera traps, we developed a quantitative index of how easily a plant could be reached by the arboreal marsupials. We did this by dividing the area around focal plants into eight wedges that extended out 1 m from the plant. A wedge was counted as occupied if there was at least one connection (i.e., a branch ≥0.5 cm in diameter) reaching from such direction. The accessibility of each plant was calculated as percent of occupied wedges surrounding it.

Measuring fruit removal and crop size.—In early January of 2009 we started monitoring fruit crop size and removal at focal plants. Each plant was visited once a week until the end of the dispersal season in late April. During each visit to a plant, we counted the total number of infructescences and randomly selected 10 of them where we counted the number of ripe fruits, the number of dry fruits (non-removed fruits persist in pedicels in this species), and the number of fruits removed (number of empty calyxes). The marsupial removes fruits by seizing them with the mouth and pulling, leaving the empty calyxes in the plant. In contrast, un-removed fruit dry in place and persist for weeks so we are confident about our estimates of fruit removal. With these data we estimated a fruit-removal index (R) per plant as

$$R_i = \sum_{t=1}^T \bar{r}_{i,t} \times F_{i,t} / T$$

where $\bar{r}_{i,t}$ is the average number of fruits removed from the 10 observed infructescences at plant i and time t , and $F_{i,t}$ is the total number of infructescences on that plant

at that time (plants were visited in a total of $T = 31$ opportunities). Similarly, we estimated an index of crop size C as

$$C_i = \sum_{t=1}^T \text{mean}(f_{i,t} + d_{i,t} + r_{i,t}) \times F_{i,t}/T$$

where f is number of ripe fruits, d are dried fruits, and r are removed fruits. These estimates of average fruit removal and crop size per week are likely to be a bit biased as some empty calyxes could last more than a week. Hence, we take these values just as relative measures to compare plants in different local environments.

Marking seeds with ^{15}N to track dispersal.—In late August of 2008, we sprayed the 20 *T. corymbosus* plants a total of five times with solutions of ^{15}N urea (99.8% atom; Cambridge Isotope Laboratories, Cambridge, Massachusetts, USA) at 0.5 g/L following methods from Carlo et al. (2009). Approximately 10 L of solution were sprayed on each spraying day, each plant receiving enough solution to wet all leaf and floral surfaces. In August, plants were at their blooming peak (Aizen 2003), and were sprayed once on five different days within a one-month period. In total, each plant received between 1 and 1.5 L of ^{15}N urea solution.

Positive controls for $\delta^{15}\text{N}$ (‰) levels in the seeds of sprayed plants came from 87 seeds collected from focal plants in March of 2009 (three to eight fruits per plant). Negative controls for natural $\delta^{15}\text{N}$ (‰) values came from 27 fruits collected from 27 normal plants (one fruit per plant). Seeds from both positive and negative controls were oven dried at 50°C, then ground and 5 mg of material packed in tin capsules for solid mass spectrometry samples (CE Elantech #240-064-40; Elantech, Lakewood, New Jersey, USA). Continuous-flow mass ratioing spectrometry was performed on all samples at the Natural Resource Laboratory at Colorado State University.

Collection and analysis of dispersed seeds.—From January through March 2009, we collected all the accessible seeds of *T. corymbosus* in the understory vegetation found within a 20 m radius from each isotopically enriched plant once each week. Seeds of *T. corymbosus* are usually defecated by *D. gliroides* along branches in strings of seeds that remain interconnected by fibers of viscin (Amico and Aizen 2000). Within the first 10 m, we mapped the location of each string of seeds in relation to the focal plant using a measuring tape and a compass. Seeds were often found clumped over small spatial scales, thus for spectrometry analyses we pooled the seeds of samples that were close to each other to reduce mass spectrometry costs. To decide which samples to pool we used a cluster analysis based on the spatial coordinates of individual samples, which resulted in groupings (clusters) of samples at distances of up to 0.5 m. Seeds collected between 10 and 20 m from the focal plant were pooled into four groups of equal

area using compass bearings: north to east, east to south, and so on (10–20 m quarters, hereafter). All seeds belonging to the same spatial cluster or quarter were ground together for mass spectrometry analyses and the isotopic signal analyzed using a Bayesian mixing model (details are available in Appendix C and scripts in the Supplement).

Weighting neighborhood effects.—The potential effect of neighbors on fruit removal and seed dispersal is not easy to quantify, since we usually don't know how animals perceive the environment. We reasoned that neighboring plants would have an influence proportional to their size but also to how far they were from the focal plant and we used a Gaussian tail to model how such influence changed with distance $h_i = \sum_j v_j z_j \times \exp(-\rho_j^2/2\lambda^2)$, where h_i is the weighted neighborhood for the i th plant, which has a total of v_j neighbors with diameter z_j located at distances ρ_j . The parameter λ controls how quickly the effect of a neighboring plant decreases with distance. We treated λ above as a parameter to be fitted in the models relating environmental variables to fruit removal, dispersal distance, and dispersal into the 10–20 m quarters.

Fruit removal and dispersal distance.—For every response variable (i.e., fruit removal, mean dispersal distance, and number of seeds dispersed to the 10–20 m quarters), we built multiple regression models with crop size index, accessibility, and weighted neighborhood index as explanatory variables. Fruit removal was modeled with a binomial distribution where the probability of removal was related via a logit link to each plant crop size index, its accessibility, and weighted neighborhood. Similarly, mean dispersal distance was modeled as a linear function of the above variables. Finally, we modeled the number of dispersed seeds arriving at the 10–20 m quarters out of the estimated number of removed seeds as a binomial, again with probability related to the three variables describing the plant local environment. All models were fitted using package *bbmle* in R (R Development Core Team 2010; software available online).⁵ We asked whether the coefficients for the explanatory variables were significantly different from zero and computed confidence intervals from likelihood profiles.

RESULTS

Identifying dispersed seeds using $\delta^{15}\text{N}$.—Seeds collected directly from focal plants (i.e., positive controls) were highly enriched with ^{15}N , and had an average $\delta^{15}\text{N}$ of $2550 \pm 1899.6\%$ (mean \pm SD). Such high $\delta^{15}\text{N}$ values contrasted with values in seeds of untreated plants (i.e., negative controls), which had an average $\delta^{15}\text{N}$ of $0.55 \pm 4.09\%$. These values of means and SDs were then used in the mixing model to estimate the number of labeled seeds in collected feces. We collected a total of 4515

⁵ <http://cran.r-project.org/web/packages/bbmle/index.html>

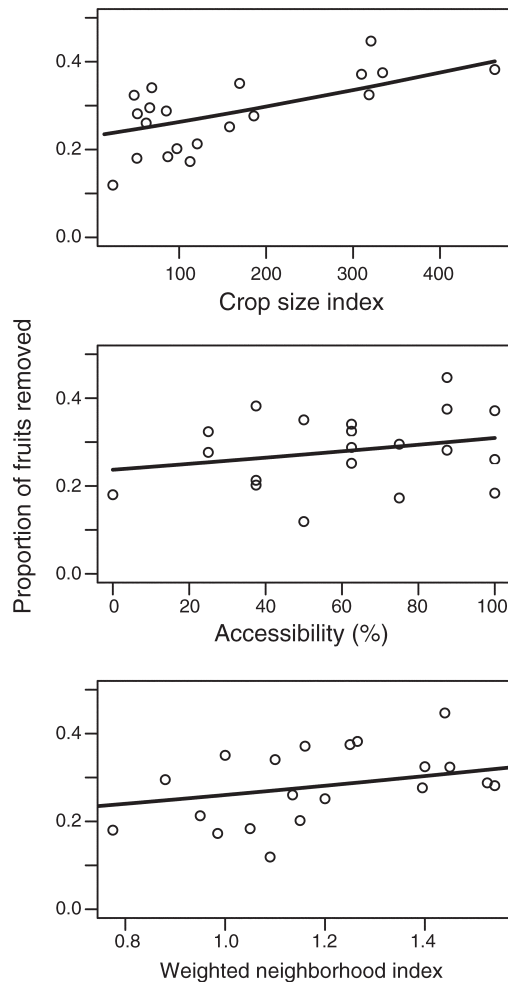


FIG. 1. Crop size and neighborhood effects on fruit removal. Lines are for significant relationships ($P < 0.05$) from a binomial regression with index of crops size, accessibility, and weighted neighborhood as explanatory variables (see *Study system* for calculations of indices). When plotting the response to a variable we set the remaining two variables at their average values.

dispersed seeds from 615 feces within 10 m of the focal plants (10-m plots). These 615 feces were then combined into 431 seed groups based on their spatial proximity. In addition, another 5730 dispersed seeds were collected from 10–20 m quarters from focal plants.

From the $\delta^{15}\text{N}$ signature of each of the 431 groups, the mixing model estimated that a total of 150 seed groups (34.8%) had at least one labeled seed. Even without any statistical analysis, the presence of at least one enriched seed was obvious in 79 of the 431 seed groups (18.3%) since their $\delta^{15}\text{N}$ values exceeded 40‰, which lie well outside the natural $\delta^{15}\text{N}$ values in plants (i.e., -15 to $+20$ ‰; Craine et al. 2009). Furthermore, the mixing model estimated that a total of 296 seeds out of the 4515 (6.56%) collected within a 10 m radius of the focal plants were dispersed from enriched plants. The

95% Bayesian credible interval for this estimate was 226 to 799 dispersed seeds. The mixing model estimated that 38 of the 69 quarters with seeds (55%) had at least one dispersed seed (16 had $\delta^{15}\text{N} > 40$ ‰), and a total of 95 dispersed seeds (Bayesian credible intervals = 63–233). Detailed results from the Bayesian analysis including convergence diagnostics, effective sample size, and credible intervals can be found in Appendix D.

Seed dispersal pattern.—Our labeling technique showed that many seeds deposited near focal plants were coming from other plants in the population (Appendix B: Fig. B1). Furthermore, multimodality in dispersal distance was apparent within the 10 m radius and also by the high number of dispersed seeds found within the 10–20 m quarters (Appendix B: Fig. B.2). These patterns of seed deposition are consistent with what has been shown in elsewhere when dispersal is mediated by animals (e.g., Aukema 2004, Russo et al. 2006, Hampe et al. 2008).

Weighted neighborhoods.—Parameter λ weighted the effect of neighboring mistletoes on fruit removal, mean dispersal distance, and number of dispersed seeds in the 10–20 m quarters. Separate analyses were run for each response variable and different but similar values of λ were found. For fruit removal, we estimated $\lambda = 0.034$ (CI = 0.000, 7.315). When looking at mean dispersal distance, λ was 0.090 (CI = 0.000, 4.001), and for the proportion of seeds dispersed to the 10–20 m quarters, we got $\lambda = 0.096$ (CI = 0.000, 0.407). These values of λ imply that the effect of neighboring plants decay very quickly with distance, being close to zero at 0.5 m from the focal plant. However, the confidence intervals for λ were very large.

Fruit removal and dispersal distances.—The arboreal marsupial readily removed fruits from focal plants (30% of available fruits on average), and we could detect an increase of fruit removal in plants that had larger crop sizes and were more accessible. Keeping other variables at average values and doubling the crop size index from 100 to 200 implies a 77.1% increase in fruit removal rate (from 0.207 to 0.367, Fig. 1), while doubling accessibility from 50% to 100% results in a 13.9% increase (from 0.272 to 0.39 Fig. 1). Furthermore, fruit removal increased with the weighted neighborhood index, with an estimated 35.9% increase when doubling neighborhood index from 0.8 to 1.6 (Fig. 1).

On the other hand, mean seed dispersal distances were not related to crop size index but were negatively related to both accessibility and the weighted neighborhood index. There was an estimated 17.2% reduction in mean dispersal distance when doubling accessibility from 50% to 100% (8.47 to 7.01 m), and a 37.2% reduction when doubling weighted neighborhood index from 0.8 to 1.6 (from 10.00 to 6.28 m), again while keeping other variables at average values (Fig. 2A, C, and E; Table 1). Finally, the number of dispersed seeds recovered in the 10–20 m quarters were negatively related to crop size index and the weighted neighborhood index but we could

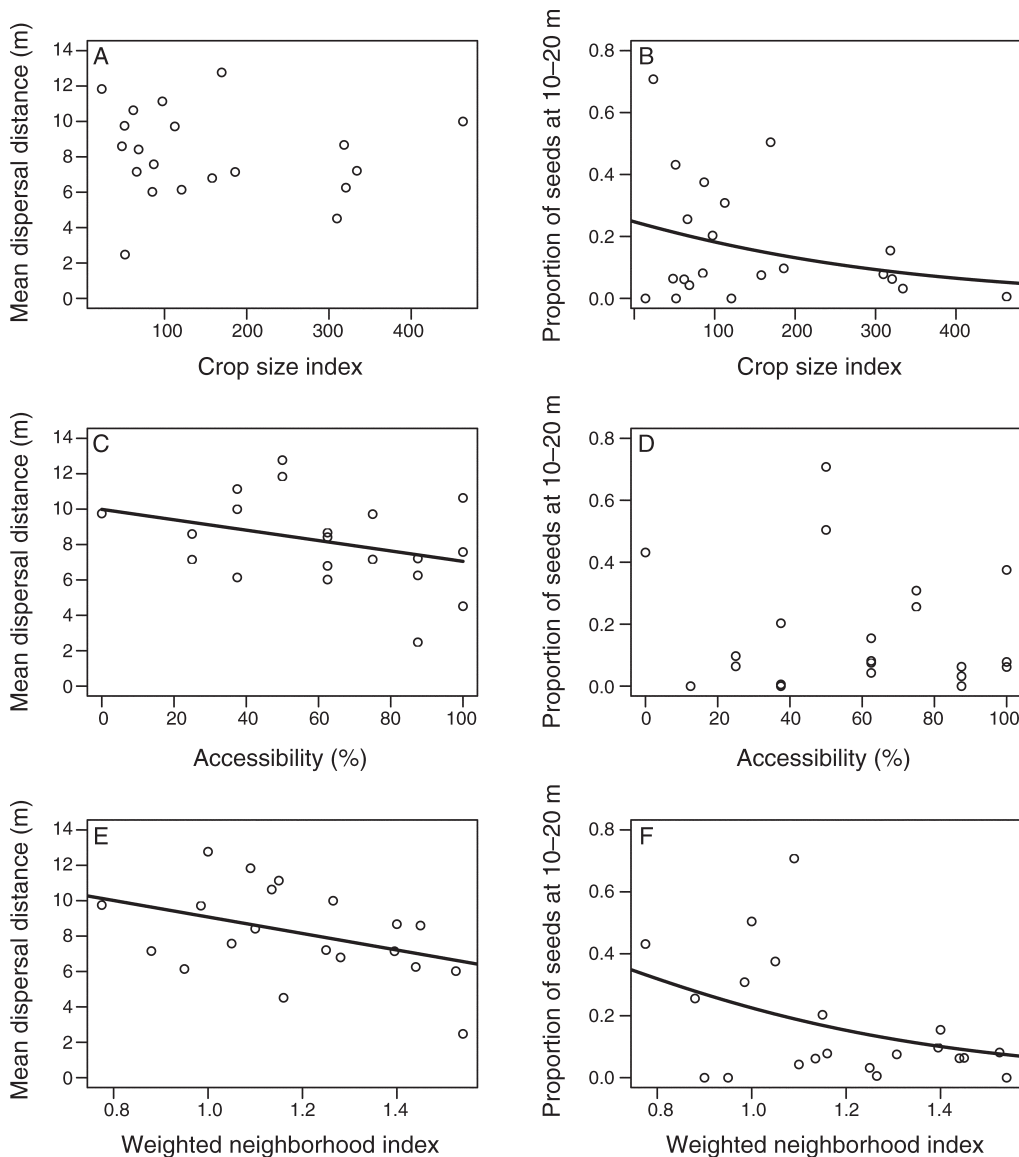


FIG. 2. Crop size and neighborhood effects on seed dispersal. Lines are for significant relationships ($P < 0.05$) from a multiple regression for (A, C, E) mean dispersal distance and (B, D, F) a binomial multiple regression for the number of dispersed seeds in the 10–20 m quarters. When plotting the response to a variable, we set the remaining two variables at their average values.

not detect and effect of accessibility (Fig. 2B, D, and F; Table 1). There was a 28% reduction in the probability of dispersal into the 10–20 m quarters when doubling crop size index from 100 to 200, and a 79.7 % reduction when doubling the weighted neighborhood index from 0.8 to 1.6 (Fig. 2F). Regression coefficients for all models, P values, and confidence intervals based on likelihood profiles are detailed in Table 1. None of the predictive variables were significantly correlated among them (Pearson’s $r < 0.28$ and $P > 0.2$ for all cases).

DISCUSSION

Our understanding of plant population dynamics has benefited from the explicit consideration of dispersal and

the spatial configuration of plants within landscapes (e.g., Levin et al. 2003, Levine and Murrell 2003) but as far as we are aware, plant population models do not include local effects on dispersal even though the potential effects of intra- and interspecific neighborhoods on seed removal and seed shadows have long been recognized (e.g., Denslow et al. 1986). Furthermore, simulation models based on simple behavioral rules predict general responses of fruit removal and seed dispersal to the degree of spatial aggregation of plants (Morales and Carlo 2006, Carlo and Morales 2008).

We found that, as predicted by theory, plants in denser neighborhoods had greater fruit removal and shorter mean dispersal distances than more isolated

TABLE 1. Linear models for fruit removal, mean dispersal distance, and proportion of seeds dispersed into the 10–20 m quarters.

Parameter	Probability of fruit removal			Dispersal distance		
	Mean	CI	<i>P</i>	Mean	CI	<i>P</i>
Intercept	–1.803	–2.418, –1.193	<0.0001	15.539	9.877, 21.123	<0.0001
Crop size index	0.218	0.142, 0.295	0.021	0.142	–0.861, 1.153	0.772
Accessibility	0.366	0.070, 0.663	<0.0001	–2.936	–6.370, 0.031	0.080
Weighted neighborhood	0.534	0.048, 1.018	0.030	–4.663	–9.032, 0.005	0.039
λ	0.034	0.000, 7.315	0.029	0.090	0.000, 4.001	<0.0001

Notes: Parameter estimates are from logit link function. Confidence intervals (CI) are estimated from likelihood profiles. *P* values are for the null hypothesis that parameters are equal to zero and were calculated from estimated standard errors.

plants. Furthermore, the probability of dispersing seeds farther away (10–20 m quarters) decreased with neighborhood density (Fig. 2). Larger crop sizes resulted in larger fruit-removal rates and smaller probabilities of dispersal into the 10–20 m quarters. Finally, plants that were more accessible for the arboreal marsupial had higher fruit removal rates and shorter mean dispersal distances. Some of these effects although statistically significant were relatively small. Ongoing studies are aimed at determining whether these effects are relevant for the spatiotemporal dynamics of the mistletoe and host plants.

Significant effects of our weighted neighborhood index were found on all response variables (fruit removal, mean dispersal distance, and dispersal into the 10–20 m quarters). The quick decay rate of the effect of neighboring plants (small λ) implies that the arboreal marsupial makes foraging decisions at relatively small scales but the large confidence intervals suggest that larger values are plausible. We do not know if we could have obtained better fits considering scales larger than 5 m radius. Ideally one could compute the neighborhood index to a fully mapped area. Furthermore, we used a square term to model the decay with distance but we have tried both a simple exponential decay and a fitted shape parameter (results not shown). The exponential gave similar results to the ones we report here but with more variability on the estimates for λ (AIC values were also similar). The estimates for the shape parameter were unstable, probably due to sample size. Presumably, a larger number of focal plants would allow a better characterization of how the influence of neighbors decreases with distance.

The scales at which we measured neighborhoods and dispersal were limited by logistical constraints, but they are almost certainly relevant to the dynamics of our study system. Mean gut passage time for mistletoe seeds ingested by the marsupial is 35.2 minutes (95% quantiles of 18.02 and 57.60 minutes; G. Amico, unpublished data). Using mark–recapture techniques, M. D. Rivarola (unpublished data) estimated average home range sizes of 1.4 ha for this marsupial in our study site. Furthermore, considering that this frugivore moves from branch to branch, we expect that most seeds will be dispersed near the mother plants. Short dispersal distances for this mistletoe will most likely result in re-

infestation of the host tree where the focal plant is located. High *T. corymbosus* loads on the understory trees can in turn result in increased mortality (Y. Sasal, unpublished data). Thus, the movement and foraging patterns of this arboreal marsupial could have important consequences for the patch and forest regeneration dynamics not only of the mistletoe but also for the whole forest understory. This type of high mistletoe infection of hosts due to positive feedbacks in local dispersal by frugivores is a common cause of host tree death (Overton 1994, Aukema 2003).

We believe that our general results are likely to hold for many plant–frugivore systems because, in general, animals will spend more time foraging in areas where fruit resources are more abundant and easier to access (Denslow et al. 1986, Sallabanks 1993, Saracco et al. 2004, García et al. 2011). Frugivores tracking fruit resources in space and time result in a characteristic positive feedback between locations of resource patches and seed deposition (Aukema and del Rio 2002, García et al. 2005). Feedbacks also result in directional seed dispersal patterns that increase the transfer of seeds across neighborhoods or patches of resource plants (Clark et al. 2004, Kwit et al. 2004).

Overall, the interplay between frugivore behavioral decisions and the spatial distribution of plants could have important consequences for population and community dynamics, especially for plant species that rely heavily on dispersal, such as mistletoes (Overton 1994, Aukema 2003). As frugivores are preferentially attracted to high-density neighborhoods, plants in such patches, particularly individuals with large crop sizes, will contribute disproportionately to the seed rain. Shorter dispersal distances in dense neighborhoods can contribute to increase patch size and density, forming areas where density-dependent processes are strong (Spiegel and Nathan 2010). Dense patches of mistletoe could increase mortality rates for hosts, creating empty patches and affecting host demographic dynamics (Worrell et al. 2005). On the other hand, plants that are less attractive to frugivores because of their crop size, isolation, or accessibility will disperse fewer seeds but at larger distances and could have an important effect on population expansion or recolonization of vacant sites, as well as increase gene flow between dense patches. Isolated fruiting individuals have been hypoth-

TABLE 1. Extended.

Probability of being dispersed to 10–20 m		
Mean	CI	P
1.268	–0.182, 2.407	0.091
–0.489	–0.716, –0.262	<0.0001
–0.182	–0.979, 0.627	0.654
–2.391	–3.661, –1.207	<0.0001
0.096	0.000, 0.407	<0.0001

esized to be important in creating “stepping stone” effects that aid on population expansion and the colonization and recolonization of sites, as well as increase gene flow between dense patches (Antonovics and Levin 1980).

Most theoretical studies set the characteristics of kernels first and then examine ecological or evolutionary consequences. Previous theoretical studies (Morales and Carlo 2006, Carlo and Morales 2008) and the empirical results presented here suggest that plant distribution patterns can feed back into the characteristics of seed dispersal of frugivore-dispersed plants. We do not expect that every small-scale detail would be relevant for larger-scale processes but it is apparent that this interplay between animal behavior and plant distribution deserves to be studied in detail and will contribute to the general goal of linking the behavior of organisms to population and community dynamics (Morales et al. 2010). Creating realistic dispersal models for plant populations is necessary if plant migrations in the face of habitat changes are to be accurately predicted and managed on real landscapes. For example, the prediction of neighborhood effects on seed dispersal distances can aid restoration efforts of endangered fruiting plant species for which fruit removal, seed dispersal, and gene flow needs to be increased. Likewise, the principles could become handy in managing invasions of undesirable species. Further theoretical and field studies should continue addressing in explicit ways the relevance of frugivore behavior for plant population dynamics.

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SUPPLEMENTAL MATERIAL

Appendix A

Illustrations of the study system (*Ecological Archives* E093-065-A1).

Appendix B

Details on fruiting neighborhoods and dispersed seeds for focal plants (*Ecological Archives* E093-065-A2).

Appendix C

Details on the mass spectrometry analysis and Bayesian mixture model for dispersed seeds (*Ecological Archives* E093-065-A3).

Appendix D

Posterior estimates for number of ¹⁵N-labeled seeds in batches of dispersed seeds mapped within the 10 m radius or collected within the 10–20 m quarters (*Ecological Archives* E093-065-A4).

Supplement

R and WinBUGS code for the mixture model (*Ecological Archives* E093-065-S1).