Indirect positive effects of a parasitic plant on host pollination and seed dispersal

Alina B. Candia, Rodrigo Medel and Francisco E. Fontúrbel

A. B. Candia, R. Medel and F. E. Fontúrbel (orcid.org/0000-0001-8585-2816), (fonturbel@gmail.com), Depto de Ciencias Ecológicas, Facultad de Ciencias, Univ. de Chile, Las Palmeras 3425, 7800024 Ñuñoa, Santiago, Chile.

Parasitic plants often have a strong fitness-impact on their plant hosts through increased host mortality and reduced or complete suppression of reproduction. *Tristerix corymbosus* (Loranthaceae) is a hemiparasitic mistletoe that infects a wide range of host species along its distribution range. Among such species, *Rhaphithamnus spinosus* (Verbenaceae) is a frequent host with a flowering and fruiting season partially synchronized with mistletoe reproductive phenology. As parasitized hosts have, in principle, a larger flower display and fruit crop size than non-parasitized hosts, we examined whether host and parasite reproductive synchrony make infected hosts more attractive for pollinators and seed dispersers than uninfected hosts. Our results showed that pollinator visit rates did not differ between parasitized and non-parasitized hosts. Conversely, seed rain was higher in parasitized than non-parasitized individuals. The number of seeds fallen under non-parasitized plants was spatially associated with crop size, while parasitized plants did not show such association. Finally, the number of seedlings of *R. spinosus* was significantly larger near parasitized than non-parasitized hosts. Our results suggest that the presence of the mistletoe might be responsible of the higher reproductive success showed by the parasitized fraction of *R. spinosus*. This effect, however, seems to be related to seed dispersal processes rather than pollination effects.

The impact of parasitism on host populations has long attracted the attention of ecologists and evolutionary biologists (Price 1980, Poulin 1997, Combes 2001). Recent conceptualization of parasitic plant–host plant systems as important components of natural communities has provided new insights on the underlying structure of complex multispecies communities, revealing an astonishing complexity in the way species interact, affect each other, and impact on ecosystem processes (reviews by Dobson and Hudson 1986, Dobson and Crawley 1994). For example, mistletoes are considered as keystone species in many forest ecosystems (Watson 2001, Aizen 2003, Press and Phoenix 2005, Nickrent 2011), as they provide valuable food resources for birds and mammals, during scarcity periods. In the same vein, the dependence of mistletoes on biotic vectors for pollination and seed dispersal facilitates genetic outcrossing which in turn influences infection capacity and long-distance dispersal (Watson 2001, Watson and Rawsthorne 2013). Even though mistletoes are known to cause negative effects on their hosts due to nutrient and water shortage, which may result in reduced or complete suppression of reproduction and increased mortality (Medel 2000, Mathiasen et al. 2008), whether parasitism affects the pollination and seed dispersal processes of the same host species remains largely unknown. In principle, mistletoes may play a pivotal role on host reproductive success by reducing host reproduction, as envisaged by traditional

models, and turning parasitized hosts more attractive to pollinators and seed dispersers, indirectly increasing their reproductive success in comparison to non-parasitized individuals. We tested this idea by focusing on a system composed by a hemiparasitic mistletoe, a shrub host species and their pollinator and seed disperser assemblage in a temperate forest of southern South America.

Tristerix corymbosus (Loranthaceae) is an evergreen hemiparasitic mistletoe that inhabits semiarid Mediterranean lands and temperate forests of South America (Amico et al. 2011). This mistletoe flowers between late fall and late spring (Aizen 2005), with a flowering peak during winter, when most plants have no flowers (Aizen 2003), becoming a valuable resource for the green-backed firecrown, *Sephanoides sephaniodes* (Smith-Ramírez 1993), which is the most important generalist pollinator of these forests. The fruiting season corresponds to the summer season, when fruits are consumed by birds (mainly the Chilean mockingbird, *Mimus thenca*) at its northern distribution (30°–37°S), and by the endemic marsupial *Dromiciops gliroides* at its southern distribution (Amico et al. 2011, Fontúrbel et al. 2012), both generalist frugivore species. *Tristerix corymbosus* parasitizes about 30 plant species, spread over 21 families (Lemaitre et al. 2012). *Rhaphithamnus spinosus* (Verbenaceae) is an evergreen thorny shrub with campanulate flowers and fleshy fruits that is commonly parasitized by *T. corymbosus*. The flowering and fruiting seasons of *R. spinosus* are partially

overlapped with that of *T. corymbosus* (Smith-Ramirez and Armesto 1994). Because of this overlap, the system is appropriate to test the idea that parasitized *R. spinosus* individuals might attract more pollinators and seed dispersers than non-parasitized plants due to a mistletoe attraction effect on mutualists, having a positive effect on their host reproduction. More specifically, we attempted to answer the following two questions: 1) are pollinator visit rate and seed rain higher in parasitized than non-parasitized *R. spinosus* shrubs? 2) Is recruitment around parasitized individuals higher than around non-parasitized hosts?

Methods

Study site and design

This study was conducted at The Valdivian Coastal Reserve (39°57′S, 73°34′W; 50 530 ha), in southern Chile. The climate is temperate-rainy with 2500 mm of annual rainfall and a mean annual temperature of 12°C. Dominant vegetation type is of Valdivian-type rainforest, including *Nothofagus dombeyi*, *Fitzroya cupressoides*, *Aextoxicon punctatum*, *Aristotelia chilensis*, *Rhaphithamnus spinosus* and *Chusquea quila* as the most representative species. At this site, five generalist frugivore species are present, four birds: *Mimus thenca*, *Elaenia albiceps*, *Turdus falcklandii* and *Columba araucana*, and one marsupial: *Dromiciops gliroides*, all of them documented as important seed dispersers of many fleshy-fruited native plants, including *T. corymbosus* (Amico et al. 2009, 2011).

We searched the study area for parasitized *R. spinosus*. We selected 20 parasitized plants and 20 non-parasitized plants to be used as control. In order to have a paired design, pairs were chosen within a 100 m radius (mean distance between parasitized and non-parasitized plants = 21.0 ± 6.0 m, mean ± 1SE, n = 20). Each plant was georeferenced using a GPS device (error = 5.0 m).

Pollination

We conducted focal observations during October 2012 on 15 parasitized plants and 15 non-parasitized plants (the remaining plants had no flowers at the sampling time). We recorded all pollinator visits to flowers during repeated 30-min intervals. We surveyed each focal plant twice, on different days, between 09 and 15 h. At each focal plant, we recorded the number of visits, visit duration (time spent by pollinators at inflorescences), and the number of flowers per plant. To make these figures comparable among individuals, we standardized visitation rate and visit duration by the number of flowers of the inflorescence per hour observation (visits × flower^{-1} and visit time × visit^{-1} × flower^{-1}, respectively).

Seed rain

We quantified seed rain under *R. spinosus* plants using circular seed traps of 48-cm diameter (covering an area of 0.19 m^2) and 1 m of height. We also counted the number of fruits (i.e. crop size) present at each individual. When plants had

≤ 20 fruits, we counted every fruit, but when plants had more than 20 fruits we randomly chose 3–5 branches to estimate the number of fruits per plant. Seed rain was estimated during two sampling periods. The first sampling was conducted from March to April 2012, and the second from November 2012 to March 2013. In the second sampling event (conducted on 19 parasitized and 19 non-parasitized plants) we performed a serial sampling on a monthly basis from November (2012) to March (2013). We standardized seed rain figures by crop size, expressing this as collected fruits per 100 plant fruits, rounded to the nearest integer.

Recruitment

We measured recruitment through sampling seedlings within four 1-m^2 quadrats randomly placed within ≤ 5 m radius around each *R. spinosus* individual, since ~84% of *R. spinosus* recruitment occurs within 5 m (Supplementary material Appendix 1 Fig. A1). The same individuals were used for seed rain measurements. We also measured the distance from each *R. spinosus* seedlings to the center of the sampling quadrant aiming to determine spatial aggregation patterns at different distances from the focal plant. All sampled seedlings were approximately one year old by January 2013.

Data analysis

Pollination

We used generalized linear models (GLM) with a negative binomial distribution (nbGLM hereafter) and a log link function to compare overall pollination rates between parasitized and non-parasitized plants. Then, we used GLMs with a Gaussian distribution to compare the standardized (visits × flower^{-1} and visit time × visit^{-1} × flower^{-1}) pollination rates.

Seed rain

Seed rain data was discrete with a leptokurtic distribution with a negative skew. We conducted a χ^2 goodness-of-fit test to determine whether seed rain data fit a Poisson or a negative binomial distribution, as these distributions are usually obtained in this kind of data (Rawsthorne et al. 2009). Then we fitted a negative binomial GLM (with a log link function) to assess the effect of *T. corymbosus* on the seed rain for the first sampling event, including host crop size as a covariate. For the second sampling event, we also used negative binomial GLMs for each monthly sampling. Then, we analyzed the temporal series using a mixed-effects GLM with a negative binomial distribution (log link function) to account for the repeated measures (i.e. monthly samplings) in our design (Zuur et al. 2009), including host crop size as a covariate.

Recruitment

We summed up the number of seedlings within the four quadrants placed in the neighbourhood (i.e. within 5-m radius) of each *R. spinosus* individual. The resulting recruitment was compared between parasitized and non-parasitized individuals using a negative binomial GLM, including host crop size (measured at the first sampling period) as a covariate.

We used two approaches to examine seedling distance to each *R. spinosus* individual. First, we estimated the degree of seedling clustering through the variance/mean ratio (values > 1 indicate aggregation), and then we conducted a χ^2 goodness-of-fit test to contrast observed and expected distributions using the actual shape (mean and dispersion) parameters (Crawley 2007). The second approach consisted on estimate the parameters of a negative binomial GLM for the number of seedlings at variable distances from the center of each *R. spinosus* individual, aiming to determine whether the number of seedlings depend on the distance to the focal plant. We used the software R ver. 2.15 to conduct all statistical analyses performed.

Spatial analyses

As we dealt with spatially structured data (i.e. plants are not randomly distributed in the space), we examined the magnitude of spatial autocorrelation for the residuals of the GLM analyses previously conducted. We calculated Geary correlograms, which provide a more accurate representation than Moran correlograms (Fortin and Dale 2005), using the software Passage ver. 2 (Rosenberg and Anderson 2011). The probability values per case were estimated using 999 permutations and five distance classes with equal number of observations per class.

Further, we examined the degree of spatial clustering of crop size and seed rain data for both sampling events (second sampling event data was analyzed separately for each month). In doing so, we used SADIE (spatial analysis by distance indices) to assess the spatial aggregation level (i.e. cluster formation) through an aggregation index I_a, and evaluated its significance level through permutations (Perry et al. 1999, Winder et al. 2001). In addition, we examined the spatial concordance between crop size and seed rain data by estimating the association index X_p, which oscillates between −1 and 1, with −1 indicating complete spatial disassociation, 0 a spatial independence, and 1 complete spatial association (Hampe et al. 2008). To assess spatial concordance, we used SADIEShell ver. 122 (Conrad 2001). We evaluated spatial aggregation for parasitized and non-parasitized plants separately. All results are presented as mean ± 1 SE, unless otherwise indicated.

Results

Pollination

Pollinator visit rates did not differ between parasitized and non-parasitized plants (nbGLM estimate = −0.15 ± 0.39 (mean ± 1SE), p = 0.69; Fig. 1a). This result was consistent after standardization by flower number (GLM estimate = 0.25 ± 0.01, p = 0.77; Fig. 1b). Similarly, visit time standardized by flower number did not reveal differences between parasitized and non-parasitized plants (GLM estimate = 0.049 ± 0.249, p = 0.770; Fig. 1c).

Seed rain

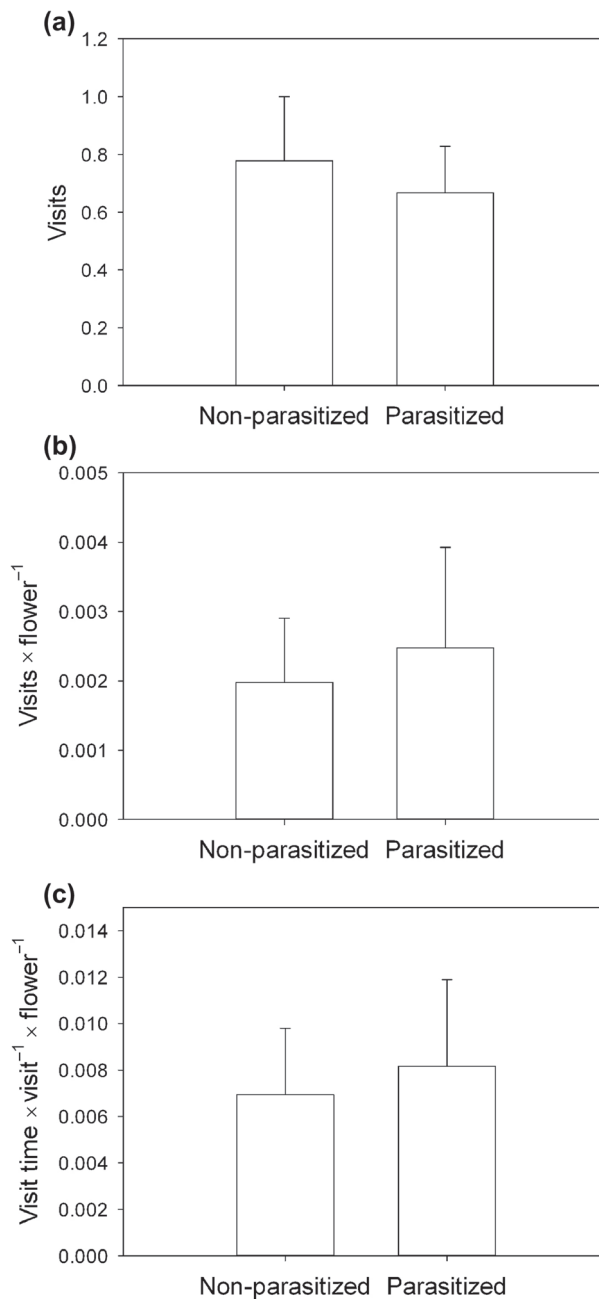Seed rain during the first sampling event (March–April 2012) fitted a negative binomial distribution, and it was

Figure 1. (a) Pollinator (*Sephanoides sephaniodes*) visits (on 30-min intervals) on non-parasitized and parasitized *Rhaphithamnus spinosus* individuals, (b) visit rates per flower, and (c) visit time per visit and flower. Bars represent mean ± 1SE.

larger under plants parasitized by *T. corymbosus* (nbGLM estimate = 3.55 ± 1.17, p = 0.006; Fig. 2) and under plants with large crop sizes (nbGLM estimate = 0.04 ± 0.01, p < 0.001). Seed rain and crop size showed a significant interaction (nbGLM estimate = −0.03 ± 0.01, p < 0.001).

We did not find a clear trend for the second sampling period (November 2012–March 2013). Overall, seed rain of parasitized and non-parasitized plants did not differ at any sampling month (nbGLM P > 0.481, except during February–March, p = 0.073, Fig. 3). When examining the whole data series, we found no difference between parasitized and non-parasitized plants (nbGLMM estimate = 0.13 ± 0.48, p = 0.574)
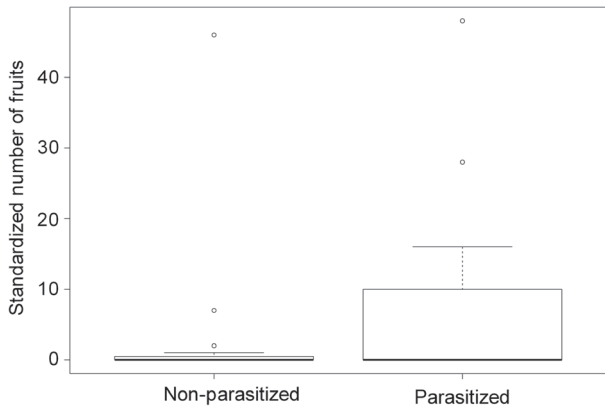
Figure 2. *Rhaphithamnus spinosus* seed rain (standardized by crop size) at parasitized and non-parasitized plants. Bars represent mean ± 1SE.
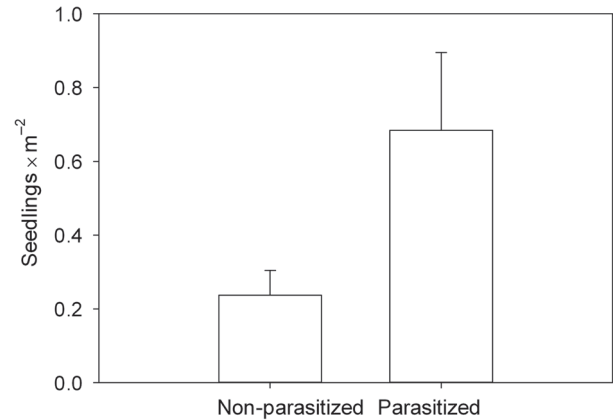

Figure 4. *Rhaphithamnus spinosus* seedlings per m² under parasitized and non-parasitized plants. The crop size of *R. spinosus* was included as covariate in analysis. Bars represent mean ± 1SE.

and no effect of host crop size on seed rain (nbGLMM estimate = $3.6 \times 10^{-5} \pm 4.6 \times 10^{-4}$, p = 0.574).

Recruitment

The number of seedlings was larger nearby parasitized than non-parasitized *R. spinosus* (nbGLM estimate = 0.865 ± 0.428, p = 0.044; Fig. 4), and crop size (included as a covariate) had no effect on this outcome (estimate = 0.001 ± 0.001, p = 0.125). Seedlings showed an aggregated distribution near *R. spinosus* regardless of its status of parasitism (Fig. 5). However, seedlings were more aggregated in parasitized than non-parasitized *R. spinosus* (ratio mean/variance, parasitized: 3.90, non-parasitized: 1.27). In both cases, the observed seedling distribution was different from the expected distribution based on a random process ($\chi^2 = 4.24$, p = 0.039 for parasitized individuals and $\chi^2 = 4.38$, p = 0.036 for non-parasitized individuals). Moreover, seedling aggregation was independent from distance to the focal plant

at both parasitized (nbGLM estimate = 0.002 ± 0.003, p = 0.386) and non-parasitized individuals (nbGLM estimate = 0.001 ± 0.003, p = 0.737).
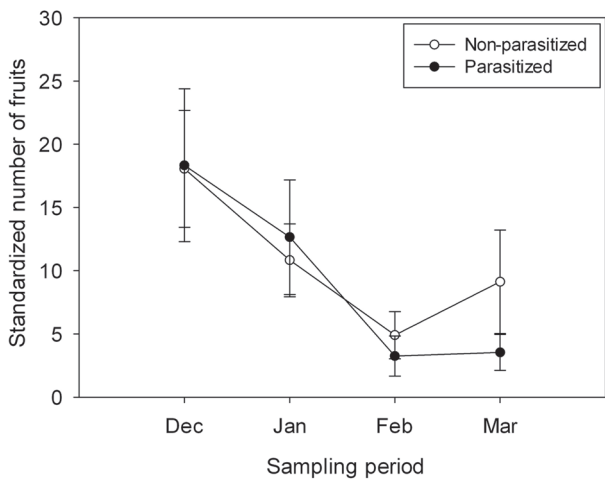

Figure 3. *Rhaphithamnus spinosus* seed rain monthly series (December 2012–March 2013) for parasitized and non-parasitized individuals. Seed rain data was standardized by crop size. Bars represent mean ± 1SE.
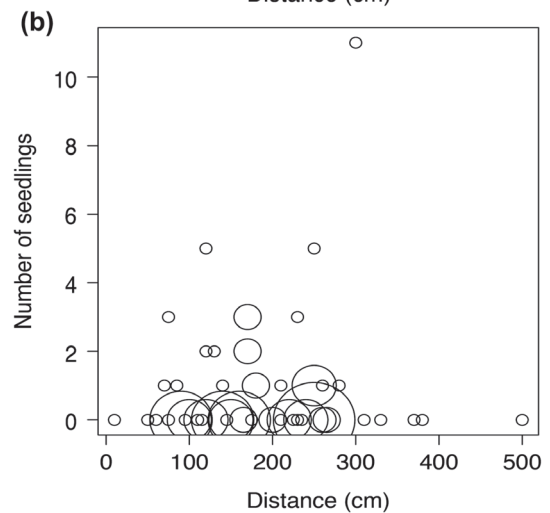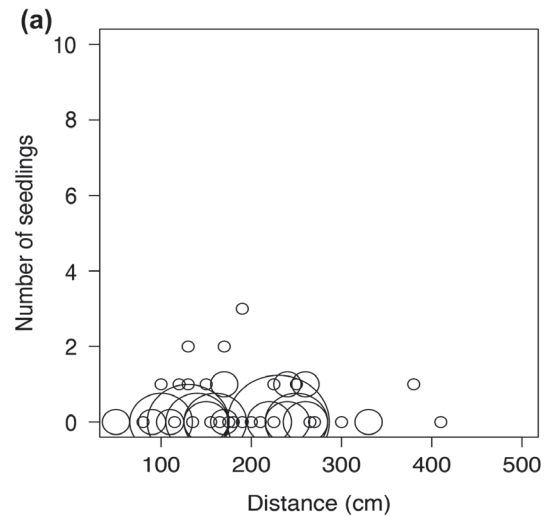
Figure 5. Seedling aggregation nearby *R. spinosus* (a) non-parasitized and (b) parasitized individuals. Bubble size represents the number of repetitions of number of seedlings-distance cases.

Spatial autocorrelation and association

We did not find a significant spatial autocorrelation for model residuals (Geary correlogram p > 0.45 on each case), supporting the assumption of spatial independence. Crop size and seed rain data were not significantly aggregated in the space, irrespective of its infection status. We further examined the spatial association between $R.$ $spinosus$ crop size and seed rain, and they were positively associated at the non-parasitized fraction only (X_p non-parasitized = 0.53, p = 0.02, X_p parasitized = −0.02, p = 0.52). During the second sampling event, we found a significant spatial association only for parasitized plants during November–December period (X_p = 0.44, p = 0.04), and marginal associations were found for non-parasitized plants during November–December (X_p = 0.42, p = 0.06) and February–March (X_p = 0.39, p = 0.07) samplings.

Discussion

Pollinator visit rates did not differ between parasitized and non-parasitized plants. The absence of effect at this may be related to the strong competition for pollinators during spring, when most plant species are flowering at the same time. This situation may be originated from a neighborhood effect, in which the wide range of floral resources available at some sites would reduce the visit probability at some focal individuals (Caruso 1999, Morales and Carlo 2006, Morales et al. 2012). In our study site, the native tree *Embothrium coccineum* was flowering simultaneously with *Tristerix corymbosus* and *Rhaphithamnus spinosus* during the pollination sampling, and we detected visits to *E. coccineum* flowers nearby seven *R. spinosus* focal individuals; indeed, visit lengths observed on three *E. coccineum* plants were larger than those observed on *R. spinosus* (unpubl. data).

Seed rain was larger at parasitized individuals at the first sampling event. However, this effect disappeared during the second sampling event. Such outcome may emerge from the fact that in the first sampling period, *T. corymbosus* showed a delayed fruiting season with a peak between February and March (i.e. having a larger temporal match with *R. spinosus*), whereas during the second sampling period the fruiting peak was between January and February, and most mistletoes had no or very few fruits in March. An important consideration made to analyze seed rain data is the potential effect of *R. spinosus*' crop size, which was included in our models as covariate, since the amount of collected fruits and seeds primarily depends on the amount of fruits available at each individual. Our results suggest that the presence of *T. corymbosus* fruits might be attracting more frugivores, which may be partially explaining the patterns observed. The positive relationship between seed rain and crop size is somewhat expected since larger crop sizes would attract frugivore species hence increasing the chance of fruit removal.

At the beginning of the second sampling event, when few ripe fruits were present at both mistletoe and host branches, the seed rain of parasitized and non-parasitized plants did not show a clear trend. On the contrary, from December to February, when ripe fruits were more abundant potentially increasing the attraction of frugivores, many other species (e.g. *Aristotelia chilensis* and *Rubus ulmifolius*) had abundant ripe fleshy fruits, which may also caused a mixed neighborhood effect (Saracco et al. 2005, Morales and Carlo 2006, Morales et al. 2012). Under this scenario, the foraging on fruits of *R. spinosus* decreased as the abundance of alternative resources increased nearby the focal plants. The last sampling series, corresponding to February–March 2013 also provides an interesting insight into the complexity of this ecological phenomenon, because as *T. corymbosus* fruits became less abundant (i.e. after the fruiting peak), parasitized hosts seems to be less attractive for frugivores.

Regarding recruitment, *R. spinosus* seedlings were more abundant and densely aggregated nearby parasitized plants. This result could mean that 1) parasitized *R. spinosus* individuals may be creating recruitment hotspots, or 2) parasitized *R. spinosus* individuals might be increasing their own recruitment. These two non-mutually exclusive outcomes may have positive implications for *R. spinosus* reproductive success, especially if the second scenario is accompanied with maternity assignment analyses using molecular techniques.

Our results showed that plant–plant parasitism is a complex ecological phenomenon, in which negative and positive interactions occur between the parasite and its host. Besides the negative effects that mistletoes may cause on their hosts (Henríquez-Velásquez et al. 2012), the net result on host reproductive success probably depends on the extent of host–parasite phenology overlap. This outcome is possible in this fauna-depauperate system, in which few generalist species interact with many plant species (Aizen et al. 2002), acting as functionally equivalent mutualists (Zamora 2000) across a variety of plant taxa. Since mistletoes are considered as keystone species on many forest ecosystems (Watson 2001), it is likely that their flowers and fruits turn hosts more attractive for the pollinators and seed dispersers that share with its hosts. This fact was clearly evidenced through the increased recruitment nearby parasitized plants, which might be generating recruitment hotspots nearby parasitized plants, which also might be positive for host's reproductive success. The study case presented here illustrates one of the many potential pathways by which plant parasites may indirectly benefit host populations. The net result of direct and indirect parasite effects on host reproductive success, however, requires quantification of the detrimental fitness-impact of parasitism on host populations, and maternity analyses that link parasitized maternal plants and nearby seedlings. With such information, we would be able to understand the pivotal role of mistletoes as determinant of negative and positive effects on plant communities.

References

Aizen, M. A. 2003. Influences of animal pollination and seed dispersal on winter flowering in a temperate mistletoe. – Ecology 84: 2613–2627.

Aizen, M. A. 2005. Breeding system of *Tristerix corymbosus* (Loranthaceae), a winter-flowering mistletoe from the southern Andes. – Aust. J. Bot. 53: 357–361.

Aizen, M. A. et al. 2002. Historial natural y conservación de los mutualismos planta–animal del bosque templado de Sudamérica austral. – Rev. Chil. Hist. Nat. 75: 79–97.

Amico, G. C. et al. 2009. The potential key seed-dispersing role of the arboreal marsupial *Dromiciops gliroides*. – Acta Oecol. 35: 8–13.

Amico, G. C. et al. 2011. Geographic variation in fruit colour is associated with contrasting seed disperser assemblages in a south-Andean mistletoe. – Ecography 34: 318–326.

Caruso, C. M. 1999. Pollination of *Ipomopsis aggregate* (Polemoniaceae): effects of intra- vs interspecific competition. – Am. J. Bot. 86: 663–668.

Combes, C. 2001. Parasitism: the ecology and evolution of intimate interactions. – Univ. of Chicago Press.

Conrad, K. 2001. SADIESHell ver. 1.22. – <www.ecologicalresearch.co.uk/kfconrad/download.htm>.

Crawley, M. J. 2007. The R book. – Wiley.

Dobson, A. P. and Hudson, P. J. 1986. Parasites, disease and the structure of ecological communities. – Trends Ecol. Evol. 1: 11–15.

Dobson, A. P. and Crawley, M. 1994. Pathogens and the structure of plant communities. – Trends Ecol. Evol. 10: 393–398.

Fontúrbel, F. E. et al. 2012. Ecological consistency across space: a synthesis of the ecological aspects of *Dromiciops gliroides* in Argentina and Chile. – Naturwissenschaften 99: 873–881.

Fortin, M. J. and Dale, M. 2005. Spatial analysis: a guide for ecologists. – Cambridge Univ. Press.

Hampe, A. et al. 2008. Spatio-temporal dynamics and local hotspots of initial recruitment in vertebrate-dispersed trees. – J. Ecol. 96: 668–678.

Henríquez-Velásquez, C. et al. 2012. Damage caused by mistletoe *Misodendrum punctulatum* Banks Ex Dc. on architecture and radial growth of *Nothofagus pumilio* (Poepp. et Endl.) Krasser forests of southern Chile. – Austral Ecol. 37: 816–824.

Lemaitre, A. B. et al. 2012. Host preference of a temperate mistletoe: disproportional infection on three co-occurring host species influenced by differential success. – Austral Ecol. 37: 339–345.

Mathiasen, R. et al. 2008. Mistletoes: pathology, systematics, ecology and management. – Am. Phytopath. Soc. 92: 988–1006.

Medel, R. 2000. Assessment of parasite-mediated selection in a host–parasite system in plants. – Ecology 81: 1554–1564.

Morales, J. M. and Carlo, T. A. 2006. The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. – Ecology 87: 1489–1496.

Morales, J. M. et al. 2012. Neighborhood effects on seed dispersal by frugivores: testing theory with a mistletoe–marsupial system in Patagonia. – Ecology 93: 741–748.

Nickrent, D. L. 2011. Santalales (including mistletoes). – In: Encyclopedia of life sciencies. Wiley.

Perry, J. N. et al. 1999. Red–blue plots for detecting clusters in count data. – Ecol. Lett. 2: 106–113.

Poulin, R. 1997. Evolutionary ecology of parasites: from individuals to communities. – Chapman and Hall.

Press, M. C. and Phoenix, G. K. 2005. Impacts of parasitic plants on natural communities. – New Phytol. 166: 737–751.

Price, P. W. 1980. Evolutionary biology of parasites. Monographs in population biology. – Princeton Univ. Press.

Rawsthorne, J. et al. 2009. A simple parametric method for reducing sample sizes in gut passage time trails. – Ecology 90: 2328–2331.

Rosenberg, M. S. and Anderson, C. D. 2011. PASSaGE: pattern analysis, spatial statistics and geographic exercise. – Meth. Ecol. Evol. 2: 229–232.

Saracco, J. F. et al. 2005. Crop size and fruit neighborhood effects on bird visitation to fruiting *Schefflera morototoni* trees in Puerto Rico. – Biotropica 37: 80–86.

Smith-Ramírez, C. 1993. Los picaflores y su recurso floral en el bosque templado de la isla de Chiloé, Chile [Hummingbirds and their floral resources in temperate forests of Chiloé island, Chile]. – Rev. Chil. Hist. Nat. 66: 65–73.

Smith-Ramirez, C. and Armesto, J. J. 1994. Flowering and fruiting patterns in the temperate rainforest of Chiloe, Chile – ecologies and climatic constraints. – J. Ecol. 82: 353–365.

Watson, D. M. 2001. Mistletoe – a keystone resource in forests and woodlands worldwide. – Annu. Rev. Ecol. Syst. 32: 568–576.

Watson, D. M. and Rawsthorne, J. 2013. Mistletoe specialist frugivores: latterday 'Johnny Appleseeds' or self-serving market gardeners? – Oecologia 172: 925–932.

Winder, R. et al. 2001. Modelling the dynamic spacio-temporal response of predator to trasient prey patches in the field. – Ecol. Lett. 4: 568–576.

Zamora, R. 2000. Functional equivalence in plant–animal interactions: ecological and evolutionary consequences. – Oikos 88: 442–447.

Zuur, A. F. et al. 2009. Mixed effect models and extensions in ecology with R. – Springer.