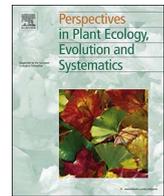


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## Research article

# Plant-animal mutualism effectiveness in native and transformed habitats: Assessing the coupled outcomes of pollination and seed dispersal

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## ABSTRACT

Most flowering plants depend on biotic pollination and seed dispersal for reproductive success. Pollination and seed dispersal are generalized mutualistic interactions, in which species with different effectiveness levels participate. However, anthropogenic habitat disturbance may hamper the impact of mutualists, jeopardizing plant establishment and recruitment. Important as it is, the effect of habitat transformation on the joint contribution of pollinators and seed dispersers to plant reproduction remains little explored. To assess the effects of habitat transformation on the effectiveness of pollination and seed dispersal processes, we studied a highly specialized system that consists of a hemiparasitic mistletoe, one hummingbird pollinator, and one marsupial seed disperser species that inhabit native and transformed habitats in southern Chile. Pollination and seed dispersal effectiveness landscapes were highly variable and did not differ between habitats. Pollinator visitation and fruit removal were higher at the transformed habitat whereas seed disperser visitation and fruit set were higher at the native habitat, probably due to differences in structure and resource availability between habitats. In consequence, and contrary to our expectations, the coupled outcome of pollination and seed dispersal was higher at the transformed habitat, suggesting that persistence of the tripartite mutualism in the overall system is benefitted from the presence of a native understory vegetation that attracts pollinators and seed dispersers and compensates for the often detrimental effects of habitat transformation.

## 1. Introduction

Pollination and seed dispersal are key ecological processes that largely influence plant reproductive success and demography (Harper, 1977). More than 90% and 70% of flowering plants in tropical forests depend on animal vectors for pollination or seed dispersal, respectively (Howe and Smallwood, 1982; Ollerton et al., 2011). As plant recruitment depends on the formation of viable seeds through the adequate deposition of pollen grains, and subsequent seed dispersal to adequate sites, the sequential coupling of animal-mediated pollination and seed dispersal is of paramount importance for plant regeneration in the face of habitat disturbance. In spite of this, most studies focus on the separate effects of pollination and seed dispersal, and the joint outcome of both mutualisms is rarely assessed in an integrated way (e.g., Gomes et al., 2014). This omission has precluded the understanding of the relative sensitivity of different mutualistic interactions to anthropogenic habitat disturbance and their consequences for plant reproduction (Neuschulz et al., 2016). One way to connect the two sequential mutualistic processes is to adopt the mutualism effectiveness

framework (Schupp et al., 2017). As defined, mutualism effectiveness results from the combination of two components: a quantitative component (i.e., number of visits and number of flowers pollinated/seed dispersed per visitation) and a qualitative component (i.e., fertilization and fruit set, germination and seedling survival). In mutualistic plant-animal interactions only a few animal species are highly effective for plant reproductive success, whereas the remaining species provide poor quality interactions (e.g., few visitations, damaged seeds after gut passage, pollen or seeds deposited in unsuitable sites) (Schupp et al., 2017; Vázquez et al., 2005). In this way, the mutualism effectiveness concept (Schupp et al., 2010, 2017) permits the assessment of intra- and inter-species variability in interaction effectiveness. This approach has been previously used to study the relative contribution of many species in one system (e.g., Rodríguez-Rodríguez et al., 2013; Rother et al., 2016), but to the best of our knowledge it has not been used to compare the effectiveness of mutualistic interactions across habitats (but see González-Castro et al., 2015; Nogales et al., 2017). Mutualism effectiveness can be assessed using effectiveness landscapes (i.e., an abstract representation of the quantitative and qualitative interaction

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components) that provide a more accurate representation of individual contributions to the total effect. In this work, we used this framework to study the way pollination and seed dispersal processes are affected by habitat transformation.

Plant-animal mutualisms are sensitive to anthropogenic disturbance (Fontúrbel et al., 2015a; McConkey et al., 2012). Human activity often causes habitat loss, fragmentation, and degradation, all of which can affect ecological interactions by modifying species abundance and the composition of species assemblages. For example, habitat fragmentation is known to alter the abundance, identity and behaviour of mutualist animal species (Figueroa-Esquivel et al., 2009; González-Varo, 2010), reducing plant recruitment and even leading to local extinction (Cordeiro and Howe, 2003; Rodríguez-Cabal et al., 2007). Less attention has been given to the effects of habitat transformation (i.e., the total or partial replacement of native vegetation by exotic species), despite being an important driver of biodiversity loss (Albert et al., 2013). Even though ecological interactions seem to respond differently to habitat transformation than to habitat fragmentation (Fontúrbel et al., 2015b), the mechanisms behind those responses are yet to be assessed. Here we reanalysed the data from Fontúrbel et al. (2015b) (freely available from the DRYAD repository: Fontúrbel et al., 2015c) to examine whether changes in the quantity and quality of mutualistic interactions visualized as effectiveness landscapes for pollination, seed dispersal and its combination, affect plant reproductive outcome.

In this work we focused on a highly specialized mutualistic system, composed by a mistletoe (*Tristerix corymbosus* (L.) Kuijt, Loranthaceae) that is solely pollinated by one hummingbird (*Sephanoides sephaniodes*) and dispersed by an endemic arboreal marsupial (*Dromiciops gliroides*) (Aizen, 2003). We hypothesized that the differences in habitat structure, microclimate conditions and resource availability between native and transformed habitats (Fontúrbel et al., 2015b; Fontúrbel et al., 2017a) will alter the quantitative and qualitative components of pollination and seed dispersal interactions. We examined pollination and seed dispersal effectiveness landscapes along a habitat transformation gradient, where *Eucalyptus* plantations gradually replace the native forest. This highly specialized mutualistic system is ideal to examine the effect of habitat transformation on pollination and seed dispersal effectiveness because the few number of species involved reduce the confounding effect of redundant species upon the overall mutualism landscape (Rother et al., 2016). We raise three questions: (1) does the overall effectiveness of pollination, seed dispersal and its combination change between habitats? (2) if so, are quantitative and qualitative effectiveness components of pollination and seed dispersal similarly altered? and (3) does plant reproductive outcome change between habitats?

## 2. Materials and methods

### 2.1. Study site

This research was conducted at the Valdivian Coastal Reserve (39°57'S 73°34'W), a 50,830-ha private owned protected area managed by The Nature Conservancy (Delgado, 2010). This Reserve is one of the largest remnants of temperate rainforest in southern South America, which is considered as a biodiversity hotspot (Mittermeier et al., 2005; Myers et al., 2000). This protected area is represented by a complex habitat mosaic that involves 47,730 ha of native forest stands (primary and secondary) and 3100 ha of transformed habitat, that consists on 12–20 years old exotic *Eucalyptus* plantations, never harvested and currently abandoned. The native habitat is dominated by *Nothofagus dombeyi*, *Nothofagus punilio* and *Eucryphia cordifolia* as canopy species, and by *Laurelia philippiana*, *Drimys winteri* and *Mitrorhia coccinea*, with sparse clumps of the native bamboo *Chusquea quila* and a few *Lapageria rosea* vines at the understory level. At the transformed habitat instead, *Eucalyptus globulus* is the only canopy species, being *Aristotelia chilensis*, *Rhaphithamnus spinosus*, *Ugni molinae*, *Luma apiculata* and *Fuchsia*

*magellanica*, *C. quila* clumps, and *L. rosea* vines the most common understory species (Fontúrbel et al., 2015b).

### 2.2. Study system

The flowering season of the mistletoe *Tristerix corymbosus* occurs from austral fall to early spring, and the fruiting season lasts from late spring to mid-summer, when *D. gliroides* activity reaches its peak because of the warm temperatures. Despite being self-compatible, *T. corymbosus* relies on biotic pollination for flower fertilization and subsequent fruit production, where *S. sephaniodes* plays a major role, along with sporadic pollination by bees (Aizen, 2005). There are two known legitimate seed dispersers of *T. corymbosus*: the Chilean Mockingbird (*Mimus thenca*) at its northern distribution range (30–37°S), and *D. gliroides* at its southern distribution area (37–42°S) (Amico et al., 2011). Despite *M. thenca* distribution goes as far as 40°S, it shifts its role as disperser > 37°S seemingly due to variation in forest structure and microclimate conditions that influence ripe fruits to remain green (in contrast to the red-coloured ripe fruits < 37°S), which makes them practically undetectable by avian dispersers (Amico et al., 2011). In terms of reciprocal dependency, this specialized system is highly asymmetric as *T. corymbosus* strictly depends on both mutualists for reproduction but mutualistic animals include more items in their diet, *S. sephaniodes* pollinating about 20% of the native flora (Smith-Ramírez, 1993) and *D. gliroides* feeding on fleshy fruits, insects and eggs (Fontúrbel et al., 2012).

We examined the coupled effect of pollination success and seed dispersal, two sequential phases of *T. corymbosus* reproductive cycle. For both phases, we estimated the quantitative and qualitative components of the mutualistic effectiveness (Schupp et al., 2017). In both cases, we recorded the quantitative component using visitation rates, which has been shown to be a good interaction proxy (Vázquez et al., 2005). Regarding qualitative components, we used fruit set as a quality proxy for pollination, as this measure represents the proportion of flowers that turn into fruits after successful fertilization. For seed dispersal, we used fruit removal as a quality proxy. Even though fruit removal is often considered as a quantitative component, the hemiparasitic biology of this species turns classic qualitative proxies such as gut treatment and seed deposition little informative. Also there are methodological limitations that preclude to accurately know the fate of dispersed seeds after the fruit is removed from the plant. For instance, the peculiar dispersal system of the mistletoe (Amico and Aizen, 2000) and the restricted locomotion of *D. gliroides* (di Virgilio et al., 2014; Gallardo-Santis et al., 2005) makes that seeds are rarely defecated in places different to host branches and stems, reducing the variation in seed survival and growth as most seeds make contact with the host surface and become established. We know that host plant species differ in quality (using adult mistletoe survival as a proxy: Fontúrbel et al., 2017b), but we have not observed important growth differences among host plants in our study site (FEF personal observation). For those reasons, and aware of the limitations involved, we decided to use fruit removal as quality component, as was previously done by Rother et al. (2016).

### 2.3. Data collection

We sampled 70 *T. corymbosus* plants during the 2012–2013 austral summer. For each sampled plant, we recorded: (1) *S. sephaniodes* visitation rate, measured using infrared camera-traps (Bushnell Trophy Cam 2011; Overland Park, KS) placed in front of each focal plant for 48 straight hours; this approach has been previously used to quantify visitation rates with good results (Fontúrbel et al., 2015b). Cameras were set in video mode (640 × 480 pixels resolution, 15 s length, 1 min interval between shots, sensor set at normal level) to record interactions. *Sephanoides sephaniodes* visitation rate was expressed as the number of visitations per flower per hour. (2) Fruit set, estimated by

counting the number of flowers (inflorescences with more than 50 flowers were sampled by tagging and counting every flower on a randomly chosen branch) during the peak of the flowering season ( $20.2 \pm 1.1$  flowers tagged on average); then, we returned at the beginning of the fruiting season (about three months later) and counted the number of fruits produced. Fruit set was then expressed as the ratio: number of fruits/number of initial flowers. (3) *D. gliroides* visitation rate, measured using camera-traps as described for *S. sephaniodes* and expressed as the number of visitations per fruit per hour; and (4) fruit removal, measured by painting ten random fruits with a non-toxic water-based acrylic paint and counting the number of remaining painted fruits five days later. Seed traps were set below sampled plants to account for fallen fruits. Fruit removal was expressed as the ratio: marked fruits removed/total marked fruits. For simplicity, pollination, seed dispersal and joint effectiveness values are represented as dimensionless scores along the results. To get a more precise estimation of plant reproductive success, we randomly sampled five fruits per plant and assessed its germination rate in Petri dishes with wet filter paper at room temperature. As *Tristerix* species have recalcitrant seeds that germinate immediately after pericarp removal with no need of prior gut passage (González et al., 2007). Further, *T. corymbosus* seeds experience a neutral (or even positive) gut treatment when are eaten by *D. gliroides*, as this marsupial has a very simple (primitive) digestive system, defecating intact seeds and hence providing high-quality seed dispersal services (Amico et al., 2009). Germination rate was calculated as the proportion of germinated seeds after five days. Therefore, we defined *T. corymbosus* reproductive success using the delayed interaction outcomes (Schupp et al., 2017), this was estimated as fruit set \* fruit removal \* seed germination rate, to obtain an index varying between 0 and 1.

#### 2.4. Habitat effect

Considering that our study area comprises a mixed landscape of native and transformed habitats, we measured its effect as the proportion of native habitat at three spatial scales defined by three non-overlapping circular rings around each focal plant: 0–50 m, 50–100 m, and 100–250 m, recording the immediate environment, the plant neighbourhood, and the foraging patch area, respectively (as described in Fontúrbel et al., 2015b). We used this approach to avoid multicollinearity among scales (García and Chacoff, 2007). Native habitat proportions were estimated using aerial imagery and digital cartography, which were intersected with the ring buffers in ArcGIS 10.1 (ESRI, Redlands CA). As thumb rule, when native habitat cover was > 50% the plant was assigned to the ‘native’ group, whereas when native cover was  $\leq 50\%$  the plant was assigned to the ‘transformed’ group. This procedure was repeated for each spatial scale, resulting in 42 plants assigned to the native habitat and 28 to the transformed habitat at the 0–50 m scale, 28 and 42 plants assigned to the native and the transformed habitats respectively at the 50–100 m scale, and 24 and 46 plants assigned to the native and the transformed habitats respectively at the 100–250 m scale. To have a detailed description of the immediate surrounding of plants, we measured the following structural features at a 2.5-m radius from focal plants: shrub cover (estimated visually), bamboo cover (estimated visually), number of stems, number of fallen logs, number of stumps, and number of natural cavities in the trees. The air temperature, relative humidity, and luminosity were recorded below sampled plants using handheld thermohygrometer and luxometer devices, respectively.

#### 2.5. Data analysis

We first elaborated effectiveness landscapes for each mutualist species. For the pollinator *S. sephaniodes* we used the number of visitations (standardized by hour and number of flowers) as quantitative measure, and fruit set as qualitative measure. For the disperser *D.*

*gliroides*, we used the number of visitations (standardized by hour and number of fruits) as quantitative measure, and fruit removal rates as qualitative measure. We used bubble plots to represent the variation of quantitative and qualitative components of pollination, seed dispersal and the combination of both interactions, using plant reproductive success (as defined above) as bubble plot size factor. Bubble plot charts allow visual representation of three variables simultaneously, two variables represent the x and y axes and the third variable is represented by the diameter (i.e., size factor) of each data point. Overall mutualistic effectiveness was estimated for each interaction by multiplying the quantitative and qualitative components, and the overall effectiveness of the combined mutualisms from the product of the two effectiveness values. Pollination and seed dispersal effectiveness values were used to construct the overall effectiveness landscape using plant reproductive success (as explained above) as bubble plot size factor.

In a second step, we constructed individual and overall effectiveness landscapes separating the native and transformed habitats at the three spatial scales previously defined. Effectiveness landscape isoclines were plotted using the R code of Jordano (2014). We tested for pairwise differences between habitats at each spatial scale using Generalized Linear Models (GLM) with a Gaussian error distribution, using each effectiveness component as response variable and habitat type as a categorical predictor. Likewise, we compared the plant reproductive success between habitats and amongst spatial scales using GLMs. In order to avoid small estimate figures, visitation rates were multiplied by 100 before performing the GLM analysis. For comparing germination rates between habitats at each spatial scale we fitted Generalized Linear Mixed Effect Models (GLMM) with a binomial error distribution, using the result of germination trials of each seed (0 = no germination, 1 = germination) as response variable, habitat type as a categorical predictor and plant ID as a random factor (Zuur et al., 2009). We estimated GLMM parameters and their significance using restricted maximum likelihood *t*-tests with a Kenward-Roger approximation to degrees of freedom (Halekoh and Højsgaard, 2014).

To assess the potential effects of habitat structure and microclimate, we used the field measurements as explanatory variables, and mutualist effectiveness and plant reproductive success as response variables. Considering that response variables did not meet the assumption of normality, we used regression trees to estimate the relative importance of structural and microclimate features. The regression tree approach is a non-parametric statistical method (part of the classification tree technique) that uses a recurring partitioning process to split data in a series of branches using thresholds that determine intermediate and terminal nodes. Specifically, we used a Random Forest classification method for branching the data. All statistical analyses were conducted in R 3.10 (R Development Core Team, 2014) using the packages tree (Ripley, 2014), mgcv (Wood, 2001), lme4 (Bates et al., 2013), lmerTest (Kusnetzova et al., 2015) and pbrtest (Halekoh and Højsgaard, 2014).

### 3. Results

*Sephanoides sephaniodes* activity ranged from zero to 37 visitations in a 48-h monitoring period (mean activity  $\pm$  SE:  $2.96 \pm 1.22$  visitations). Fruit set ranged from 55 to 100%, with a mean of  $84.44 \pm 2.19\%$ . *Dromiciops gliroides* activity ranged from zero to nine visitations in a 48-h monitoring period (mean activity  $\pm$  SE:  $1.19 \pm 0.38$  visitations). Fruit removal trials were highly variable, ranging from 0 to 100%, with a mean of  $37.83 \pm 6.14\%$  of the fruits removed in a five-day period. We depicted this information in effectiveness landscapes for both mutualisms (Fig. 1). The pollination effectiveness landscape (Fig. 1a) shows that most plants received less than 0.02 visitations \* flower<sup>-1</sup> \* h<sup>-1</sup> but most plants had fruit set values > 80%. On the other hand, the seed dispersal effectiveness landscape (Fig. 1b) showed that most plants received less than 0.01 visitations \* fruit<sup>-1</sup> \* h<sup>-1</sup> and removal rates < 60%, only 15% of the sampled plants had fruit removal rates > 80%. When pollination and

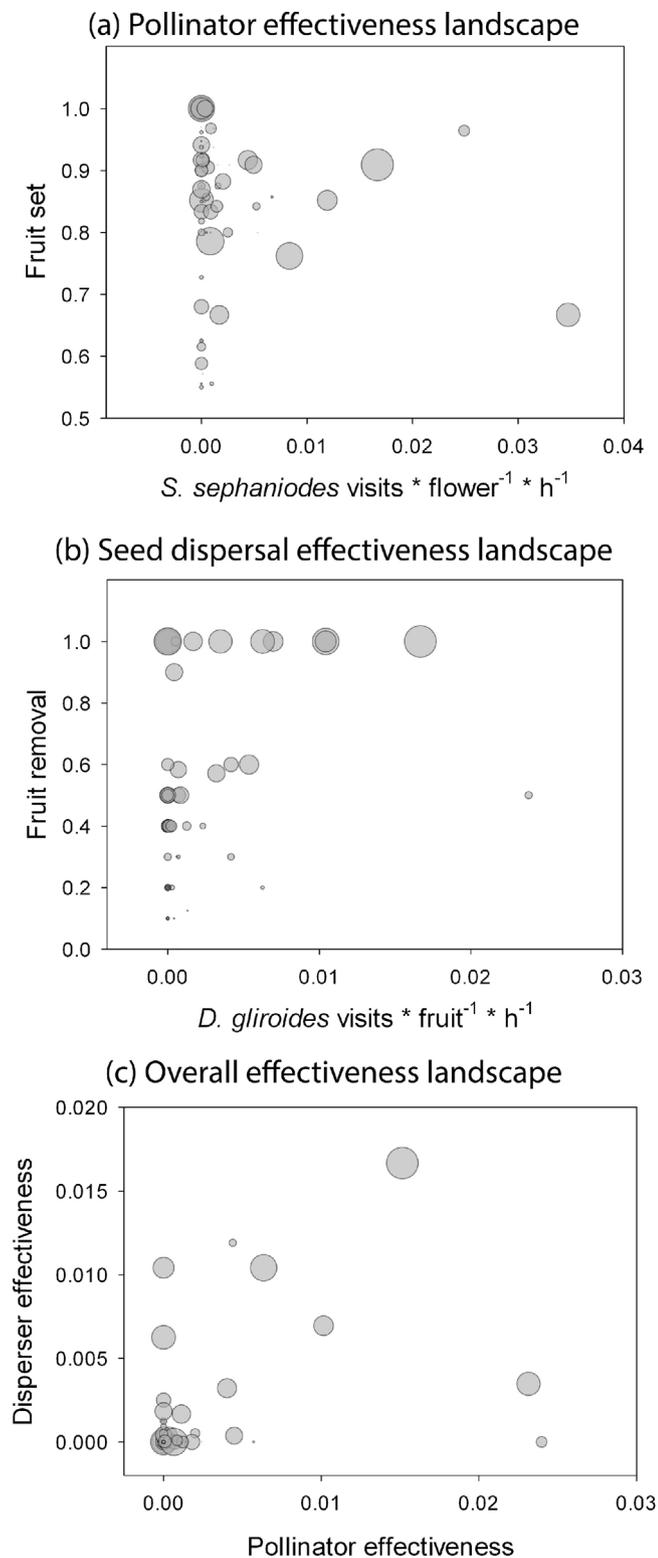


Fig. 1. Effectiveness landscapes for: (a) pollination, (b) seed dispersal, and (c) the combination of both mutualisms. Bubble size represents individual plant's reproductive success.

seed dispersal effectiveness were combined to obtain the overall mutualistic effectiveness landscape (Fig. 1c), most plants showed low to moderate effectiveness values, but a few plants had high effectiveness

values for pollination or for both pollination and seed dispersal.

Globally, mutualistic effectiveness did not differ between native and transformed habitats (Table 1). Examining pollination (Fig. 2a), quantitative and qualitative components of pollination effectiveness did not differ between habitats, excepting by marginal differences in visitation rates at the 0–50 m scale and in fruit set at the 50–100 m scale. The resulting effectiveness landscape shows that visitation rates are higher at the transformed habitat whereas fruit set is higher at the native habitat. Likewise, regarding the seed dispersal effectiveness landscape (Fig. 2b), visitation rate did not differ between habitats albeit fruit removal rate was marginally higher in the transformed habitat at the 100–250 m scale and borderline significant at the 0–50 m scale. The resulting effectiveness landscape shows that visitation rates are higher in the native habitat whereas fruit removal is higher in the transformed habitat. When the effectiveness of the two mutualistic interactions were combined into a single landscape (Fig. 2c), neither pollination nor seed dispersal differed between habitats at any scale, excepting by a marginal and positive difference in pollination in the transformed habitat at the 0–50 m scale.

Seed germination rates differed between habitats being higher at the transformed habitat, although differences are statistically significant only at the 0–50 m scale (Table 2). Further, plant reproductive success was larger at transformed habitats, irrespective of the spatial scale that was considered, although statistical differences were marginal (Table 3). Examining potential effects of habitat structure and microclimate on the mutualistic system, shrub cover, and number of stems (when over than 32.5% is covered) influenced pollinator effectiveness (Fig. 3a). Disperser effectiveness, in turn, was influenced by a complex cascade of factors (Fig. 3b) starting by shrub cover that is subsequently influenced by luminosity when cover > 77.5%. Below this percentage the number of stems becomes relevant and when the number of stems is below 5.5, humidity becomes relevant. Finally, plant reproductive success was mainly influenced by relative humidity, but when this feature exceeds 76.5% luminosity becomes relevant. Below 76.5% humidity the number of stems and temperature were relevant (Fig. 3c).

#### 4. Discussion

The effectiveness of both pollination and seed dispersal was similar between native and transformed habitats. Here we found a situation in which a highly specialized plant-pollinator-disperser system is capable to persist in an abandoned *E. globulus* plantation with similar effectiveness values. Such absence of differences may result from the compensation of quantitative and qualitative components between pollination and seed dispersal. *Sephanoides sephanioides* made more visits and *D. gliroides* removed more fruits at the transformed habitat, whereas *D. gliroides* made more visits and more *T. corymbosus* flowers yielded fruits at the native habitat. Although those differences were non or marginally significant, habitat transformation had a differential effect on the effectiveness components of both mutualisms. Habitat disturbance at the transformed habitat may alleviate pollen limitation due to the increased number of pollinator visits, as found in forest fragments (Magrath et al., 2013). Despite the larger *S. sephanioides* visitation rates at the transformed habitat, fruit set was lower compared to the native habitat. This may result from the large flower availability at the transformed habitat (Fontúrbel et al., 2017a), potentially conditioning more but shorter visits. Contrarily, *D. gliroides* performed fewer visits to *T. corymbosus* at the transformed habitat but removed more fruits. This could result from abundance and diversity of fleshy fruits at the transformed habitat that make *D. gliroides* individuals to spend more time feeding on a single plant or in groups of neighbouring plants (Fontúrbel et al., 2017b), instead than differences in local abundance (Fontúrbel et al., 2014). This appears to be a more general phenomenon, as seed removal rates seem to be insensitive to habitat

**Table 1**

Generalized Linear Model summary for pollination (a, b), seed dispersal (c, d), and overall (e, f) effectiveness comparing native and transformed habitats at three spatial scales.

(a) Pollination – visitation rates						
Variable	Scale 0–50 m		Scale 50–100m		Scale 100–250m	
	Estimate (SE)	P value	Estimate (SE)	P value	Estimate (SE)	P value
Intercept	0.113 (0.085)	0.189	0.172 (0.107)	0.112	0.194 (0.116)	0.098
Habitat(transf)	0.246 (0.135)	0.073	0.066 (0.138)	0.636	0.027 (0.143)	0.851
(b) Pollination – fruit set						
Variable	Scale 0–50 m		Scale 50–100 m		Scale 100–250 m	
	Estimate (SE)	P value	Estimate (SE)	P value	Estimate (SE)	P value
Intercept	0.860 (0.019)	< 0.001	0.879 (0.022)	< 0.001	0.851 (0.025)	< 0.001
Habitat (transf)	–0.039 (0.029)	0.181	–0.057 (0.029)	0.051	–0.009 (0.031)	0.747
(c) Seed dispersal – visitation rates						
Variable	Scale 0–50 m		Scale 50–100 m		Scale 100–250 m	
	Estimate (SE)	P value	Estimate (SE)	P value	Estimate (SE)	P value
Intercept	0.159 (0.062)	0.013	0.242 (0.075)	0.002	0.234 (0.082)	0.006
Habitat (transf)	0.012 (0.098)	0.904	–0.131 (0.097)	0.181	–0.107 (0.101)	0.291
(d) Seed dispersal – fruit removal						
Variable	Scale 0–50 m		Scale 50–100 m		Scale 100–250 m	
	Estimate (SE)	P value	Estimate (SE)	P value	Estimate (SE)	P value
Intercept	0.321 (0.051)	< 0.001	0.316 (0.063)	< 0.001	0.269 (0.067)	< 0.001
Habitat (transf)	0.143 (0.081)	0.080	0.103 (0.082)	0.209	0.165 (0.083)	0.049
(e) Overall effectiveness – Pollination						
Variable	Scale 0–50 m		Scale 50–100 m		Scale 100–250 m	
	Estimate (SE)	P value	Estimate (SE)	P value	Estimate (SE)	P value
Intercept	0.095 (0.068)	0.168	0.150 (0.086)	0.084	0.169 (0.093)	0.072
Habitat (transf)	0.200 (0.108)	0.067	0.042 (0.111)	0.705	0.010 (0.114)	0.932
(f) Overall effectiveness – Seed dispersal						
Variable	Scale 0–50 m		Scale 50–100 m		Scale 100–250 m	
	Estimate (SE)	P value	Estimate (SE)	P value	Estimate (SE)	P value
Intercept	0.102 (0.048)	0.0375	0.170 (0.058)	0.005	0.153 (0.064)	0.019
Habitat (transf)	0.037 (0.076)	0.627	–0.088 (0.076)	0.249	–0.054 (0.079)	0.491

disturbance when generalist frugivores are involved (Farwig et al., 2017). Also, some mistletoes present higher fruit set and fruit removal values but no visits; as the flowering and fruiting periods of *T. corymbosus* are quite long, it is possible that those plants were visited before or after we conducted the trap-camera monitoring.

Whereas *S. sephaniodes* is capable to disperse long distances across heterogeneous landscapes (Magrach et al., 2013), *D. gliroides* is a movement-restricted species due to its high dependence on forested habitats (Fontúrbel et al., 2010). Nevertheless, despite being originally described as an old-growth forest specialist (Hershkovitz, 1999), recent evidence indicates that this ancient marsupial has a plastic response to

habitat disturbance being capable to persist in many secondary forests (Fontúrbel et al., 2012), and exotic-tree dominated stands (Salazar and Fontúrbel, 2016), as long as they retain some structural features such as a thick shrub cover, and bamboo presence. Therefore, we can expect a context-dependent response of the seed dispersal services provided by *D. gliroides*, depending on the ‘suitability’ determined by habitat structure, resource availability and plant species diversity (Schupp, 2007). The assessment of habitat structure and microclimate features showed that an environmental features can influence pollination and seed dispersal effectiveness, as well as the resulting plant reproductive success, suggesting that the context-dependency proposed by Schupp

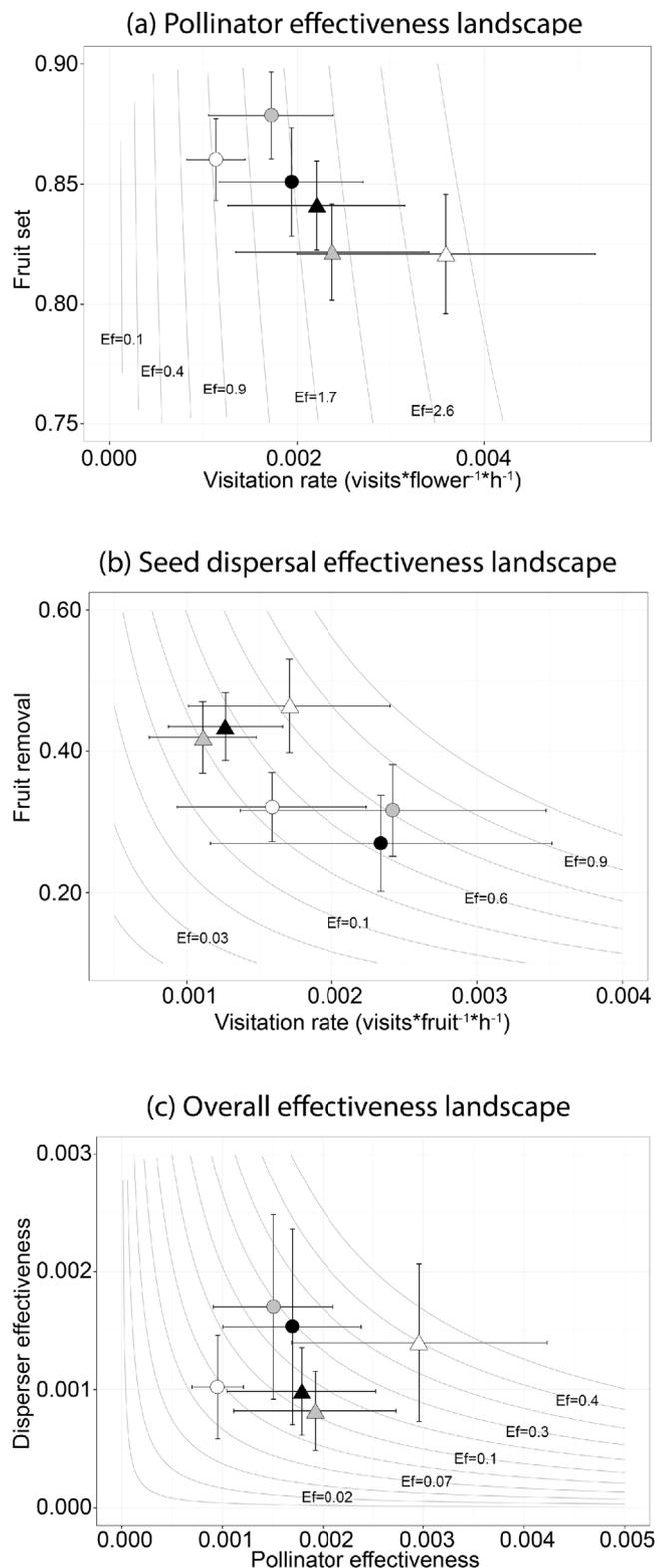


Fig. 2. Influence of habitat transformation on effectiveness landscapes (presented as mean  $\pm$  1SE) for: (a) pollination, (b) seed dispersal, and (c) the combination of both mutualisms. Triangles represents native habitat and circles represent transformed habitat. White shapes correspond to 0–50 m scale, grey shapes to 50–100 m scale, and black shapes to 100–250 m scale.

(2007) for seed dispersal could be also extrapolated to pollination and to the overall reproductive success. Our results suggest that shrub cover (providing movement paths and alternative resources), light incidence (speeding up flower opening and fruit ripening) and humidity (increasing germination probabilities avoiding seeds to dry) provide most of the context for *T. corymbosus* pollination and seed dispersal.

Mistletoes experienced a four-fold higher overall mutualistic effectiveness when surrounded by *E. globulus* – associated vegetation, which seems to be largely attributable to increased pollination (see Fig. 2c). In fragmented landscapes habitat loss is acknowledged as the main cause of interaction disruption (Hadley and Betts, 2012; Rodríguez-Cabal et al., 2007), but in transformed habitats the underlying mechanisms seem to be by far more complex than previously thought. For instance, habitat transformation did not disrupt or reduce pollination or seed dispersal effectiveness as expected accordingly to what we know from a habitat fragmentation context (e.g., Magrath et al., 2013; Rodríguez-Cabal et al., 2007). Transformed habitats are known to hold a nested subset of the species pool of the native habitat, which are usually generalists (Barlow et al., 2007), which may explain the persistence of some interaction with low dependency for the animal species.

Our results may emerge from the presence of a well-developed understory vegetation at the transformed habitats, which might be favouring the interactions with *T. corymbosus* in two ways: (1) by providing a denser structure due to the high shrub and stem densities, as well as to the abundant bamboo plants (Rodríguez-Cabal and Branch, 2011); and (2) due to the presence of dense mistletoe clumps surrounded by shade-intolerant plants, providing large flower and fruit displays (Fontúrbel et al., 2015b; Fontúrbel et al., 2017a). Regarding the first point, transformed habitats have a less complex canopy structure, but they have very thick understory vegetation, which may be providing movement pathways and shelter sites for small-bodied species (Bro-Jørgensen, 2008), such as *D. gliroides*. Habitat disturbance can impact on disperser's behaviour in function of forest cover and resource availability, leading to changes in seed dispersal distances (Breitbach et al., 2012; Breitbach et al., 2010). Regarding the second point, the availability of food resources may also influence visitation rates (Fontúrbel et al., 2017a) and dispersal distances (Morales et al., 2012), potentially altering plant community structure (Sasal and Morales, 2013). Despite mutualistic effectiveness appears to be unaffected at the transformed habitat, there are some altered processes behind the patterns observed. First, the dense mistletoe aggregations found in transformed habitats (Fontúrbel et al., 2015b; 2017b) suggest that a mixed neighbourhood of shade-intolerant plants providing abundant food resources (mainly composed by *Aristotelia chilensis*, *Rhaphithamnus spinosus* and *Ugni molinae*) alter mistletoe recruitment at transformed habitats. Second, altered dispersal distances and dense plant aggregations may convey long-term costs to *T. corymbosus*, such as reduced gene flow at the landscape scale and increased inbreeding depression. Third, variation in biotic and abiotic conditions between native and transformed habitats may represent contrasting selective scenarios for *T. corymbosus* (Fontúrbel and Medel, 2017).

In our study system, the spatial structure may also play an important role as groups of neighbouring plants influence foraging decisions (Fontúrbel et al., 2017a) and aggregation patterns depend more on host plants than dispersal distances (Fontúrbel et al., 2017b). These findings are consistent with theoretical model expectations (Carlo and Morales, 2008), suggesting that what we found at the Valdivian Coastal Reserve could be extrapolated to other systems. Particularly, our results could be extensive to other parasitic plant species worldwide, as mistletoes usually rely on few pollinator and seed disperser species (Mathiasen et al., 2008; Watson and Rawsthorne, 2013). Thinking in more generalist systems (where redundant species occur), we expect to find

**Table 2**  
Generalized Linear Mixed Effect Model summary for seed germination between native and transformed habitats, at three spatial scales.

(a) Scale 0–50 m, Plant ID variance = 1.943, BIC = 336.2				
Variable	Estimate	Std error	z value	P value
Intercept	1.125	0.305	3.694	< 0.001
Habitat(transf)	1.063	0.500	2.126	0.034
(b) Scale 50–100 m, Plant ID variance = 1.958, BIC = 337.6				
Variable	Estimate	Std error	z value	P value
Intercept	1.019	0.369	2.764	0.006
Habitat (transf)	0.859	0.479	1.796	0.073
(c) Scale 100–250 m, Plant ID variance = 2.138, BIC = 340.6				
Variable	Estimate	Std error	z value	P value
Intercept	1.371	0.427	3.211	0.001
Habitat (transf)	0.261	0.508	0.513	0.608

compensation among species in addition to potential quantity-quality compensation as those described here, keeping in mind that sub-optimal plant recruitment may occur as result of effectiveness differences among redundant species (Calviño-Cancela and Martín-Herrero, 2009; González-Castro et al., 2015). The way such compensation occurs in redundant mutualistic systems (i.e., if they are context-dependent or independent regarding the nature of the compensation and the net cost-benefit balance) is yet to be assessed in terms of mutualistic effectiveness (Schupp, 2007).

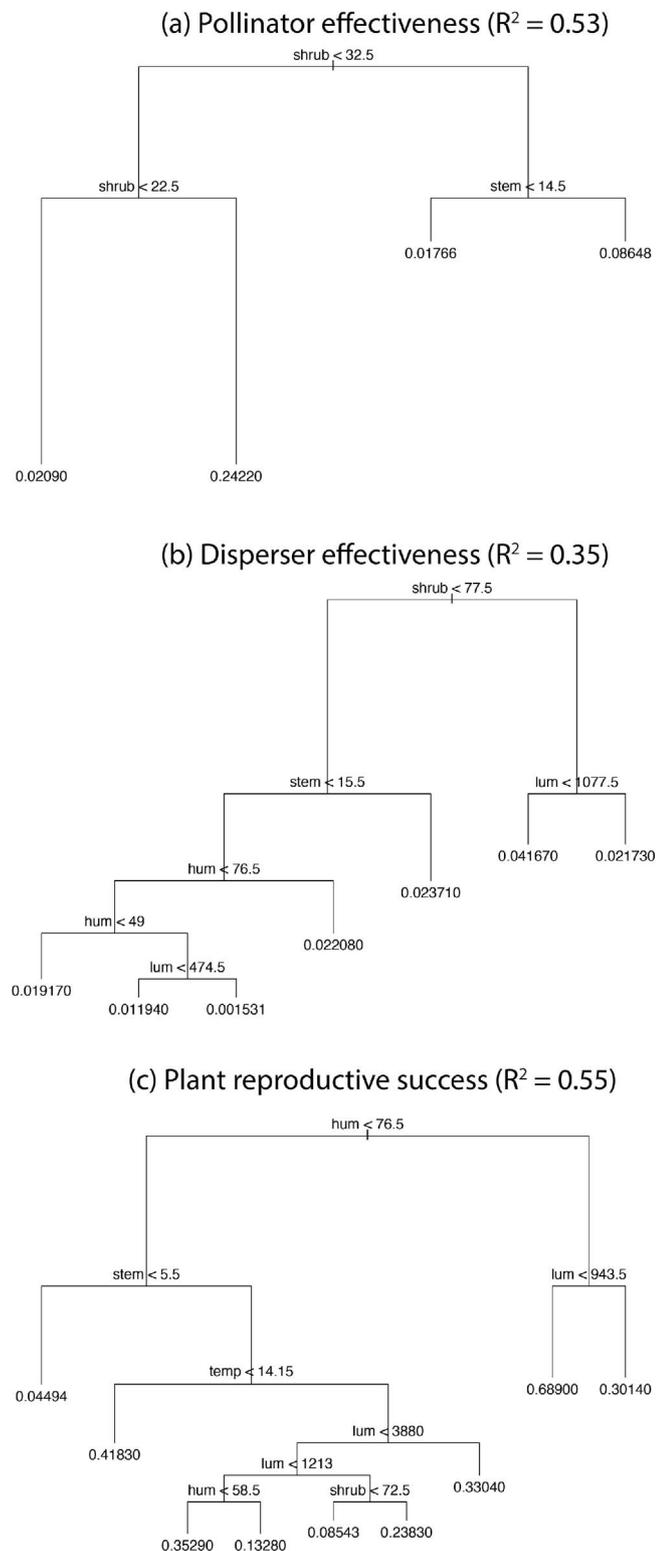
## 5. Conclusions

Overall mutualism did not vary between native and transformed habitats. The absence of differences in effectiveness between habitats

resulted from a different composition of quantitative and qualitative components for pollination and seed dispersal. While pollinator visitation rates and fruit removal rates were higher at the transformed habitat, fruit set and seed disperser visitation rates were higher at the native habitat, resulting in a quality-quantity compensation, that favoured pollination at the transformed habitat and seed dispersal at the native habitat. Such changes were related to structural and microclimate features of habitats. In addition, despite the similar overall effectiveness, quantity-quality compensation may have profound implications for plant demography, leading to counterintuitive results such as the higher plant reproductive success at the transformed habitat. As a final caveat, quality proxies used here (especially for seed dispersal) constitute a simplified view of what is happening in nature. Because of limitations inherent to our study system we were unable to

**Table 3**  
Generalized Linear Model summary for plant reproductive success (fruit set x fruit removal x germination) between native and transformed habitats, at three spatial scales.

(a) Scale 0–50 m				
Variable	Estimate	Std error	t value	P value
Intercept	0.204	0.037	5.514	< 0.001
Habitat(transf)	0.114	0.059	1.945	0.056
(b) Scale 50–100 m				
Variable	Estimate	Std error	t value	P value
Intercept	0.198	0.046	4.321	< 0.001
Habitat (transf)	0.086	0.059	1.447	0.152
(c) Scale 100–250 m				
Variable	Estimate	Std error	t value	P value
Intercept	0.173	0.049	3.530	0.001
Habitat (transf)	0.117	0.061	1.933	0.057



**Fig. 3.** Regression trees of habitat structure and microclimate variables against: (a) pollinator effectiveness, (b) disperser effectiveness, and (c) plant's reproductive success. Pseudo- $R^2$  values are shown in parentheses.

assess other quality sub-components (e.g., pollen loads, seed survival and seedling growth), which might provide a more comprehensive assessment of the actual effects of habitat transformation on plant-animal mutualisms.

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