Increased resource availability prevents the disruption of key ecological interactions in disturbed habitats

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Abstract. Anthropogenic disturbance can modify habitat structure and resource availability, potentially disrupting ecological interactions. This issue may be critical for pollination and seed dispersal, which determine natural regeneration. The mistletoe Tristerix corymbosus is almost exclusively pollinated by a hummingbird (Sephanoides sephaniodes) and dispersed by a marsupial (Dromiciops gliroides). We examined the extent to which human-induced habitat change and resource availability influence the interaction rate of this plant–pollinator–seed disperser system, along a forest transformation gradient (from native forest to exotic plantations). We estimated visitation rates of S. sephaniodes and D. gliroides on 70 T. corymbosus mistletoes using camera traps. We related visitation rates to habitat structural features and resource availability (flowers and fruits of the mistletoe and the neighborhood) using spatially explicit models. Sephanoides sephaniodes and D. gliroides visitation rates responded positively to shrub and bamboo cover, moss abundance, and mistletoe spatial arrangement. Pollination and seed dispersal interactions were sensitive to the flower and fleshy-fruit neighborhoods, being variable across months. Further, D. gliroides showed a non-random spatial association with fleshy-fruited plants. A larger sunlight incidence on disturbed habitats may prevent the disruption of key ecological interactions by increasing resource availability. This effect would result from the presence of shade-intolerant plants, which are benefited by sunlight exposure. Patches of disturbed habitat may enhance landscape heterogeneity, providing complementary resources to the native remnants.

Key words: habitat transformation; plant–animal interactions; resource neighborhood; southern Chile; spatial structure; sunlight exposure; temperate rainforest.

INTRODUCTION

Habitat structure and resource availability have an important role in the maintenance of plant–animal interactions by determining plant performance, animal behavior, and interaction probabilities (Cordeiro and Howe 2003, González-Varo 2010, Garcia et al. 2011, Albrecht et al. 2012, Breitbach et al. 2012a). However, anthropogenic disturbance caused by selective logging and habitat transformation may modify extensively the original setting where interactions do occur (Valiente-Banuet et al. 2015, Neuschulz et al. 2016). Interacting species may respond in different ways to habitat disturbance depending on the size, structure, and composition of the remaining habitat (e.g., Garcia and Chacoff 2007, Breitbach et al. 2012b, Albrecht et al. 2014, Fontúrbel et al. 2015a), which can largely influence resource availability and distribution (González-Varo 2010, Rey and Alcantara 2014). Responses to human disturbance are usually mediated by key forest structures.
(e.g., perching branches and tree cavities) that may become limiting at disturbed habitats (Reem and Löhmus 2011). Larger sunlight exposure produced by selective logging and the replacement of canopy species by monocultures of exotic trees may favor shade-intolerant shrubs (Dalling and Hubbell 2002), which usually have large flower and fruit displays (Valladares and Niinemets 2008). Human-altered habitats tend to be structurally simpler and may provide greater resource availability, which may compensate, at least in part, for the loss of habitat quality due to an increased habitat heterogeneity (Tscharntke et al. 2012).

Pollination and seed dispersal interactions play a key role in the reproductive biology of most flowering plants (Bascompte and Jordano 2007, Neuschulz et al. 2016). This is particularly relevant in temperate forest habitats, in which animal pollinator and seed disperser animals rely on strongly seasonal resources (Jordano 1987), and over 70% of the flowering plants depend on biotic pollination and seed dispersal (Ollerton et al. 2011). The South American temperate rainforests (SATFs) is a species-depauperate endemism-rich ecosystem due to its biogeographic isolation. At these forests, ~70% of its native flora depends on animal mutualists for reproducing (Aizen et al. 2002). However, the rapid deforestation and fragmentation that SATFs is currently facing (Echeverria et al. 2006) is likely to disrupt such plant–animal interactions (Rodríguez-Cabal et al. 2007).

Altogether with habitat fragmentation, the SATF is affected by habitat degradation due to selective logging and the replacement of native trees by exotic ones with commercial purposes. Here, we examined the extent to which human-induced change in habitat structure and resource availability influence the interaction rate of a three-species mutualistic interaction of the SATF composed by the hummingbird Sephanoides sephaniodes, the marsupial Drimiciops gliroides, and the mistletoe Tristerix corymbosus. Sephanoides sephaniodes and D. gliroides are known to be negatively affected by habitat fragmentation (Rodriguez-Cabal et al. 2007, Magrach et al. 2012), but we know little about their responses to changes in habitat structure and resource availability that follow habitat degradation/transformation, and the consequent formation of gaps with more sunlight exposure.

To gain insight into that problem, we studied pollination and seed dispersal rates along a habitat transformation gradient, which ranges from native forest to transformed habitats, with a large variation in structure and resource availability. As forest gaps and exotic tree-dominated stands have larger sunlight incidence, favoring shade-intolerant species that provide more diverse and abundant flowers and fruits, we hypothesize that the increased resource offer in disturbed habitats compensates for structural differences.

**METHODS**

**Study site**

We conducted this research at the Valdivian Coastal Reserve (39°57' S, 73°34' W), a 50,530-ha private protected area managed by The Nature Conservancy (Delgado 2010), which protects ~50% of the Valdivian rainforest ecosystem in Chile. The Valdivian rainforest ecosystem is considered as a biodiversity hotspot due to their high degree of endemism and being threatened by human actions as well (Myers et al. 2000, Mittermeier et al. 2005). At the Valdivian Coastal Reserve, there is a habitat mosaic composed by native forest stands, and transformed habitat stands consisting of abandoned exotic Eucalyptus globulus plantations (planted 12–20 yr ago; not managed and never harvested) with abundant regrowth of native understory vegetation (Fig. 1). Both habitat types are neighboring and highly intertwined, as native forest replacement was conducted on the most accessible areas, leaving intact native vegetation remnants in non-accessible areas.

Native forest and transformed (i.e., abandoned E. globulus plantation with regrowth of native understory vegetation) habitats differ in terms of structure. There are larger shrub patches at the transformed habitat, whereas bamboo cover, stem density, fallen logs, and natural cavities are common at the native habitat (details are presented in Appendix S1: Table S1). Canopy at the native habitat is dominated by Nothofagus dombeyi, N. pumilio, and Eucryphia cordifolia, whereas the exotic E. globulus is the only canopy species at the transformed habitat, leaving the understory more exposed to sunlight. Understory vegetation at the native forest is dominated by Laurelia philippiana, Drimys winteri, and Mitratia coccinea, with sparse clumps of the native bamboo Chusquea quila and a
few Lapageria rosea vines. At the transformed habitat, understory vegetation is dominated by Aristotelia chilensis, Rhaphithamnus spinosus, Ugni Molinae, Luma apiculata, and Fuchsia magellanica (all shade-intolerant fleshy-fruit species), thick C. quila clumps, and abundant L. rosea vines climbing on the E. globulus stems.

Study species

We focused our research on a very specialized mutualistic system composed by a hemiparasitic mistletoe that interacts with two native vertebrates: a hummingbird and a relict marsupial. The Green-Backed Firecrown (Sephanoides sephanoides, Trochilidae) pollinates about 20% of the native flora of the SATF (Smith-Ramírez 1993). The monito del monte (Dromiciops gliroides, Microbiotheriidae) is a generalist species that feeds on fruits, eggs, and insects (Fontúrbel et al. 2012), and it is known to be the legitimate disperser of at least 16 species of native plants (Amico et al. 2009). Both mutualist animals are capable to interact with many plant species, but the mistletoe Tristerix corymbosus (Loranthaceae) depends almost exclusively on
S. sephaniodes for pollination and on D. gliroides for seed dispersal (Aizen 2003, 2005, Amico et al. 2011). By choosing this highly specialized plant, we avoid confounding effects of other redundant pollinator or seed disperser species, a situation rarely found in natural populations. Further, T. corymbosus has a major role in plant–plant facilitation, as the presence of this mistletoe increases pollination and seed dispersal rates of co-flowering/co-fruiting hosts (Candia et al. 2014). Therefore, its presence in disturbed habitats could accelerate natural vegetation recovery by enhancing plant recruitment.

**Visitation rates and habitat structure**

We located, tagged, and georeferenced 298 T. corymbosus focal plants along the study area, from which we selected 70 focal plants, corresponding to all plants that presented both flowers and fruits during the fieldwork period. In this case, we consider each mistletoe plant as a replicate. Focal mistletoes were located along a habitat disturbance gradient, with some mistletoe clumps at the disturbed areas and other randomly distributed plants at the non-disturbed area (a KMZ file to facilitate visualization of the spatial distribution of the sampled plants is available from Data S1). The surrounding habitat type of each focal mistletoe is unique and difficult to characterize as a dichotomous variable (native or transformed). Therefore, we used the approach described by Fontúrbel et al. (2015b) to characterize the habitat surrounding each mistletoe, using a 250-m buffer from each focal plant and quantified the proportion of native and transformed habitat within it. Based on that assessment, 37% of the mistletoes were located in areas with dominant native vegetation (>50% of cover) and 63% in areas with dominant transformed vegetation (Appendix S1: Table S2).

To quantify mutualists’ activity, we placed infrared camera traps (Bushnell Trophy Cam 2011, Overland Parks, Kansas, USA) set in video mode (15 s length, 640 x 480 pixel resolution, trigger with 1-min delay) at each focal plant. Camera traps are a cost-effective approach to study plant–animal interactions, providing accurate results with minimum observer interference (Lucero et al. 2014). Each camera was operated for 48 h at each focal plant, making a total cumulative effort of 3360 camera-hours. This approach was previously used to quantify visitation rates with good results (Fontúrbel et al. 2015b). Camera-trap monitoring on focal plants was conducted within a week to ensure that environmental conditions are comparable. To quantify the outcome of both pollination and seed dispersal services, we estimated fruit set (i.e., the fraction of flowers that yielded fruits) and fruit removal (based on a sample of marked fruits) rates.

To quantify habitat structure, we recorded the following structural variables at a 2.5-m radius from each focal plant: (1) shrub cover, (2) bamboo (C. quila) cover, (3) stem density, measured as the number of stems with diameter at breast height >1 cm, (4) the number of fallen logs, (5) the number of stumps, (6) the number of natural cavities, (7) moss abundance (as a categorical variable with three levels: absent, scarce, and abundant), and (8) fern abundance (categorical variable: absent, scarce, and abundant).

**Visitation rates and resource availability**

Tristerix corymbosus has a peculiar phenology pattern adapted to interact with their pollinator and seed disperser species (Aizen 2003). Flower buds develop from January to March, and open flowers are available from March to October (reaching its peak in August). Unripe fruit develop from November to January, and ripe fruits are available from January to March. Resource availability for S. sephaniodes was quantified as the number of T. corymbosus open flowers available. We conducted two flower assessments for this purpose. First, we counted and monitored (using camera traps, as explained above) T. corymbosus flowers from February to March, but in this occasion we were unable to quantify the flowering neighborhood as there were few co-flowering species. In a second assessment, we repeated the counting and monitoring procedures during fall–winter (late March and early August) when other species co-flower with T. corymbosus. Regarding fruit availability for D. gliroides, it was quantified at two levels: (1) T. corymbosus’ crop size and (2) the abundance of other fleshy-fruit resources located within a 2.5-m radius from each focal plant. The crop size of T. corymbosus was estimated by counting all ripe fruits during February and March, when most fruit ripe and reach its peak abundance. As co-fruiting plants have different phenologies, we counted ripe fruits repeatedly.
from November to March on a monthly basis (unripe fruits were counted but not considered in this analysis since they are unlikely consumed) to capture resource variability in time.

To study the spatial association between *D. gliroides* and fleshy fruits in detail, we captured 10 *D. gliroides* individuals (five at native forest and five at transformed habitats), following the methodology of Fontúrbel and Jimenez (2009) and complying with the care and handle guidelines of the American Society of Mammalogists (Sikes et al. 2011). At each habitat, we set a 6 × 8 trapping grid (a total of 48 live traps per habitat), arranged 10 m from each other. Traps were baited with fresh banana slices and a mixture of peanut butter and mackerel. The Chilean Agriculture and Livestock Bureau (SAG) authorized animal capturing (resolution 8291). Those captured individuals were fitted with 0.5 g ATS A2415 telemetry transmitters, which were glued to the animal’s fur using a non-toxic acrylic glue (Fontúrbel et al. 2010); transmitters were not removed as they drop during molting.

Due to the short battery life of transmitters (up to 20 d), we conducted an intensive tracking for 12 d (12–24 February 2014). Individuals were intensively tracked from 23 to 05 h, coinciding with *D. gliroides’* most active period (Fontúrbel et al. 2014). To minimize location error, bearings were simultaneously taken by two teams within a 10-min interval. To reduce GPS-associated error, we defined six fixed points per habitat type, with an error ≤3 m. We used two ComSpec R1000 receivers (Communication Specialists, Orange, California, USA), two ATS three-element Yagi antennas (Advanced Telemetry Systems, Isanti, Minnesota, USA), two digital compasses (Bushnell Optics, Overland Parks, Kansas, USA), and two Garmin GPS Map 62s units (Garmin Co., Olathe, Kansas, USA).

During the telemetry tracking, we recorded and georeferenced every plant showing ripe fleshy fruits using a Garmin GPS Map 62s unit (≤4 m error); we recorded plant species and the number of fruits for each plant. Plant searching area corresponded to the live-trapping grid area plus a 100-m buffer. The fact that hummingbirds cannot be mist-netted and fitted with telemetry transmitters due to the very high mortality rate associated with specimen manipulation precluded us to conduct this analysis for pollination.

### Data analysis

To assess the effects of the structural features measured on *S. sephaniodes* and *D. gliroides* visitation rates, we fitted spatially explicit generalized additive models (GAMs), with Poisson error distribution and a log-link function. Generalized additive models included the structural features as linear terms (similarly as in a generalized linear model analysis), and a spline non-linear term containing the Universal Transverse Mercator coordinates of each focal plant to account for the spatial structure, as mistletoes are not regularly distributed along the study area. We tested our models for overdispersion following Zuur et al. (2009), but no overdispersion was detected. To examine the relationship between the interaction outcome measures (i.e., fruit set and fruit removal rates, arcsine-square-root-transformed), we fitted spatially explicit GAMs with a Gaussian error distribution, including a spline term accounting for the spatial structure.

We also used spatially explicit GAMs with Poisson error distribution (as explained above) to assess the potential effect of *T. corymbosus* flower and fruit availability on *S. sephaniodes* *D. gliroides* visit rates, respectively. We also examined the effect of a mixed flowering/fruiting neighborhood (i.e., the other flowering/fleshy-fruiting species nearby *T. corymbosus*) on the *S. sephaniodes–T. corymbosus* and *D. glioides–T. corymbosus* interactions. Models for flower availability were fitted using the *S. sephaniodes* visitation rates as the response variable, and the following linear predictors terms: (1) the number of *T. corymbosus* open flowers, (2) the number of open flowers of the neighboring flowering plants, and (3) the interaction between *T. corymbosus* and the flowering neighborhood; the non-linear spatial term was included in all cases. Separate models were run for the March and August datasets. Likewise, models for fruit availability were fitted using the following linear terms: (1) *T. corymbosus* crop size values for the peak ripening period (February–March), (2) the total number of ripe fruits of the fruiting neighborhood, and (3) the interaction between *T. corymbosus* and the fruiting neighborhood; the non-linear spatial term was included in all cases. Separate models were run for the January, February, and March datasets.

Telemetry locations were estimated with two to three bearings within a 10-min interval, separated...
at least for 20°, using the software LOAS 4.0 (Ecological Software Solutions, Zurich, Switzerland). For each tracked individual, we generated a set of random locations (in the same number of actual locations) within each home range (home ranges estimated using a 95% fixed kernel estimator, following Fontürbel et al. 2010), using the Hawth’s Tool extension in ArcGIS 10.1 (ESRI, Redlands, California, USA). For each location (actual or random), we calculated (1) the distance to the nearest plant and (2) the average distance to all plants, using the Hawth’s Tool extension. We compared both distances between actual and random locations, through a generalized linear mixed model (GLMM), using tracked individuals as a random factor to account for inter-individual variability (Zuur et al. 2009). All values are presented as mean ± 1 standard error (SE). Statistical procedures were conducted in R 3.10 (R Development Core Team 2014), using the packages gstat (Pebesma 2004), mgcv (Wood 2001), mpmcorrelogram (Matesanz et al. 2011), ncf (Bjornstad 2013), and lme4 (Bates et al. 2013).

**RESULTS**

Visitation rates and habitat structure

We recorded 207 *Sephanoides sephaniodes* and 83 *Dromiciops gliroides* effective visits (i.e., with physical contact between hummingbirds and flowers, and with fruit consumption by *D. gliroides*) at the 70 monitored plants. There was little concordance between mutualist animals regarding the structural features influencing visitation rates. *Sephanoides sephaniodes* responded to bamboo cover, the number of stems, the abundance of dead wood (i.e., fallen logs and stumps), and moss abundance. *Dromiciops gliroides* responded to shrub cover and moss abundance. Moss abundance was a significant factor explaining the interaction with *Tristerix corymbosus* for both mutualist animals. On the contrary, natural cavities and ferns had no influence on visitation rates. The spatial configuration of the focal plants had a significant influence on visitation rates of both mutualists, but it was stronger for *S. sephaniodes* (Table 1). Pollination success (using fruit set as a proxy: 84.44% ± 1.43%) was not influenced by any of the structural features measured or by the spatial structure. However, seed dispersal success (using fruit removal as a proxy: 37.83% ± 4.01%) was significantly lower when ferns were scarce (GAM estimate = −0.398 ± 0.166, *P* = 0.019).

| Variables          | *Sephanoides sephaniodes* | *Dromiciops gliroides* |
|--------------------|---------------------------|------------------------|
| Shrub cover        | 0.025 (0.029)NS           | 0.025 (0.007)**       |
| Bamboo cover       | 0.110 (0.046)*            | 0.001 (0.002)NS       |
| No. of stems       | 0.215 (0.096)*            | −0.001 (0.001)NS      |
| Fallen logs        | 1.773 (0.712)             | 0.069 (0.183)NS       |
| Stumps             | 1.763 (0.464)**           | −1.178 (0.650)†       |
| Cavities           | −2.128 (1.553)NS          | −8.334 (30.010)NS     |
| Moss (abundant)    | −4.858 (1.542)**          | −1.343 (0.686)*       |
| Moss (scant)       | −5.203 (1.604)**          | 0.103 (0.548)NS       |
| Fern (abundant)    | −1.511 (3.279)NS          | −0.259 (0.599)NS      |
| Fern (scant)       | −1.853 (3.366)NS          | 0.032 (0.520)NS       |
| Spline (X, Y)      |                          | *χ² = 75.63***        |
|                    |                           | *χ² = 17.67**         |

Notes: Poisson generalized additive model linear estimates are presented (standard error is shown in parentheses). The spatially explicit non-linear term spline (X, Y) represents the effect of the spatial configuration.

Significance codes: NS, not significant; †*P* < 0.1, *P* < 0.05, **P* < 0.01, ***P* < 0.001.

Visitation rates and resource availability

During the first flower assessment (February–March), the number of open flowers of *T. corymbosus* did not account for *S. sephaniodes* visitation rates (GAM estimate = 0.001 ± 0.002, *P* = 0.618) but the spatial structure influenced significantly the hummingbird visitation rates (spline [X, Y], *χ² = 24.09, *P* < 0.001; Fig. 2a, b). During second flower assessment (late March and August), *S. sephaniodes* visitation rates responded positively to the number of flowers (GAM estimate = 0.002 ± 0.001, *P* = 0.013 for March; GAM estimate = 0.007 ± 0.002, *P* < 0.001 for August); in both cases, there was a significant (*P* < 0.001) effect of the spatial structure. Similarly, the number of ripe fruits of *T. corymbosus* did not account for *D. gliroides’* visitation rates (GAM estimate = 0.003 ± 0.004, *P* = 0.392), but plant spatial structure influenced the mammal visitation rates to the mistletoes (spline [X, Y], *χ² = 24.45, *P* = 0.034; Fig. 2c, d).

Regarding the influence of the other flowering plants (i.e., the mixed flower neighborhood) on *S. sephaniodes* visitation rates, during late March the number of flowers of either *T. corymbosus* (256 ± 23, *N* = 74) or the flowering neighborhood (composed by *Lapageria rosea* [5 ± 1, *N* = 41], *Fuchsia magellanica* [2625 ± 1939, *N* = 2], and...
Eucryphia cordifolia (853 ± 623, N = 3) contributed positively to the visitation rates of *S. sephaniodes*, but their interaction had a negative effect. Contrarily, during August, only the number of *T. corymbosus* flowers (122 ± 12, N = 77) contributed positively to the visitation rates of *S. sephaniodes*, and there was no effect of the flowering neighborhood (in this case, composed only by *L. rosea* [2 ± 1, N = 29]) or their interaction (Table 2). In all cases, the spatial structure had a significant (*P* < 0.001) effect on the visitation rates.

The influence of other plants with fleshy fruits (i.e., the mixed fruit neighborhood) on *D. gliroides* visitation rates was variable across months. Fruit neighborhood reached its peak at February, when the fleshy fruits of *Aristotelia chilensis* and *Rhaphithamnus spinosus* constituted the bulk of the available ripe fruits (Appendix S1: Fig. S1). During January and February, the availability of other fleshy fruits negatively affected *D. gliroides* visits on *T. corymbosus*, but in March (when the number of ripe fruits decays), there is a positive effect of the interaction between *T. corymbosus* and the other fruiting plants (Table 3). In addition, the spatial structure of the fleshy-fruited plant neighborhood.

### Table 2. Effects of flowering neighborhoods on *Sephanoides sephaniodes* visitation rates.

| Period | Effect | Estimate  | *P*-value |
|--------|--------|-----------|-----------|
| March  | M      | 4.4 × 10⁻³| 0.045     |
|        | N      | 2.5 × 10⁻³| <0.001    |
|        | M × N  | -5.1 × 10⁻⁶| 0.001     |
| August | M      | 0.009     | 0.001     |
|        | N      | 0.161     | 0.978     |
|        | M × N  | -0.037    | 0.549     |

*Note: The effects of the resource availability of the mistletoe (M) *Tristerix corymbosus*, the accompanying fruiting neighborhood (N) mainly composed by *Lapageria rosea*, *Fuchsia magellanica*, and *Eucryphia cordifolia*, and its interaction (M × N) are presented, after fitting Poisson generalized additive models.*

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Fig. 2. Spatially explicit representation of the variation in (a) number of *Tristerix corymbosus* flowers, (b) number of *Sephanoides sephaniodes* visits, (c) number of *T. corymbosus* flowers, (d) number of *Dromiciops gliroides* visits, generated upon the geographical coordinates of each focal mistletoe. For each case, a scale of the bubble size is provided in a box at the upper right corner.
also influenced the mammal visitation rate (spline \( [X,Y], \chi^2 = 35.37, P < 0.001 \)).

We obtained 43–72 effective locations for D. gliroides (63 ± 5 locations [mean ± 1 SE]; see Appendix S1: Fig. S2 for details) during telemetry tracking. We generated an equal number of random locations for each tracked individual within their home ranges. We only found three Mitraria cocinea plants with a total of 45 ripe fruits at the native forest habitat. At the transformed habitat, however, we found 110 plants of eight species with thousands of ripe fruits available (Appendix S1: Table S3). Due to the low number of ripe fruits available in the native forest habitat, the spatial analysis was restricted to the transformed habitat only.

Dromiciops gliroides locations were significantly closer to the fleshy-fruited plants than expected by chance (i.e., compared to the random locations), considering the distance to the nearest plant (GLMM estimate = 3.37 ± 1.31, \( P < 0.001 \)) as well as the average distance to all plants (GLMM estimate = 7.34 ± 1.49, \( P < 0.001 \)). Repeating this analysis with the most abundant fleshy-fruited species individually, we found the same pattern for Gaultheria phillyreifolia (nearest plant: GLMM estimate = 8.85 ± 1.93, \( P < 0.001 \); average distance to all plants: GLMM estimate = 8.36 ± 1.50, \( P < 0.001 \)) and T. corymbosus (nearest plant: GLMM estimate = 6.05 ± 1.92, \( P = 0.001 \); average distance to all plants: GLMM estimate = 5.93 ± 1.48, \( P < 0.001 \)). This pattern was met only when considering the average distance for R. spinosus (GLMM estimate = 5.85 ± 1.53, \( P < 0.001 \)) and A. chilensis (GLMM estimate = 8.93 ± 1.76, \( P < 0.001 \)).

**Discussion**

We found that pollination and seed dispersal were related to different habitat features, being moss abundance the only feature in common, which is particularly scant at the transformed habitat. Altogether with habitat structure, resource availability of both *Tristerix corymbosus* and *Dromiciops gliroides* visitation rates. Disturbed habitats present a simpler structure with less deadwood and lower moss abundance, but they are more exposed to sunlight. Consequently, those habitats present many shade-intolerant shrubs (e.g., *Aristotelia chilensis*, *Rhaphithamnus spinosus*, *Ugni molinae*), which typically have large flower and fruit displays. Native forest canopy is composed by large trees and precludes shade-intolerant species to grow. While moss abundance, bamboo cover, dead wood (i.e., stumps and fallen logs) abundance, and the number of natural cavities decreased with habitat disturbance, the number of flowers and fruits followed the opposite trend.

*Sephanoides sephaniodes* visitation rates increased with the number of stems, fallen logs, and stumps, whereas *D. gliroides* visitation rates increased only with shrub cover. The cover of the native bamboo, *Chusquea quila*, increased *S. sephaniodes* visitation rates (leaves from this bamboo are used by *D. gliroides* for nest building), but did not affect *D. gliroides* visitation rates despite being a key factor for its occurrence at the landscape scale (Rodríguez-Cabal and Branch 2011). The only common variable explaining visitation rates of *S. sephaniodes* and *D. gliroides* was moss abundance, which is used as nesting material by both species (Franco et al. 2011, Osorio-Zuñiga et al. 2014). Moreover, the pollination outcome (i.e., fruit set) was not influenced by any of these structural features, whereas seed dispersal outcome (i.e., fruit removal) was lower when ferns (also used as a nesting material by *D. gliroides*) were scarce.

The occurrence of *S. sephaniodes* and *D. gliroides* was negatively affected by habitat fragmentation, particularly by the avoidance of deforested habitats (Rodríguez-Cabal et al. 2007, Fontúrbel et al. 2010, Magrach et al. 2012). However, in the
absence of spatial discontinuities (i.e., deforested habitats), the interaction of the hummingbird and marsupial species with \( T. \text{corymbosus} \) appears to be determined mainly by the spatial configuration of the plants rather than by the flower or fruit availability per se. This may be particularly relevant for \( S. \text{sephaniodes} \) because, as most hummingbirds, they memorize resource locations and systematically return to those sites for feeding (González and Vásquez 2006). \( T. \text{corymbosus} \) spatial configuration is shaped by \( D. \text{gliroides} \) (García et al. 2009) due to the high dependence of this mistletoe on the disperser behavior. Moreover, \( D. \text{gliroides} \) visitation rates are influenced by fruit availability, potentially creating a positive feedback that would lead to denser mistletoe aggregations in those places with large fruit availability, creating recruitment hotspots (Fig. 3). Then, \( S. \text{sephaniodes} \) is more likely to visit those dense plant aggregations than small groups or isolated plants. The importance of alternative resources for the visitation rates of pollinator and seed disperser species was contingent on the month. When alternative resources are abundant, they have a negative effect on visitation rates to \( T. \text{corymbosus} \), but when they become scarce, they have a synergistic effect that increases visitation rates on \( T. \text{corymbosus} \) due to a positive neighborhood effect as reported in Argentina (Morales et al. 2012). Given that habitat fragmentation at the study area is negligible, it is likely that \( D. \text{gliroides} \) establish foraging areas at transformed stands, but concentrate their nesting sites at neighboring native remnants (Salazar and Fontúrbel 2016). This is confirmed by the spatial association found between \( D. \text{gliroides} \) locations and fleshy-fruited plants at the transformed habitat.

Our results provide a mechanistic explanation on the resource-structure compensation. The creation of temporal forest gaps due to selective logging, or permanent light conditions due to habitat transformation, opens a recruitment opportunity for shade-intolerant species, which are typically fast but weak competitors (Valladares and Niinemets 2008). Therefore, those shade-intolerant species produce large displays of flowers and fruits to attract pollinators and seed dispersers (Cortés and Uriarte 2012), aiming to ensure their reproduction.

Fig. 3. Schematic explanation of the positive feedback between \( Dromiciops \text{gliroides} \) and \( Tristerix \text{corymbosus} \), mediated by sunlight exposure and the fruiting neighborhood.
before being displaced by other species (i.e., slow but strong competitors such as large trees).

The alteration of certain structural features due to anthropogenic disturbance is likely to be compensated by enhanced resource availability, maintaining key interactions such as pollination and seed dispersal. Hence, logged or transformed habitats neighboring native vegetation remnants could be benefited from greater landscape heterogeneity (Tscharntke et al. 2012, Salazar and Fontúrbel 2016). Abandoned productive lands are becoming increasingly common worldwide (Hobbs et al. 2014). These “simplified” habitats could be benefited from a more diverse and abundant resource offer that would not only prevent the disruption of key interactions, but also may contribute to accelerate natural recovery of degraded lands. Abandoned productive areas and degraded lands could be managed to enhance landscape heterogeneity and promote the maintenance of ecological interactions, beyond than the maintenance of the intervening species themselves.

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DATA ACCESSIBILITY

Original data are available from the figshare digital repository https://doi.org/10.6084/m9.figshare.4654240 (Fontúrbel, Salazar & Medel 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1768/full