



An exotic magnet plant alters pollinator abundance and behavior: a field test with a native mistletoe

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Received: 24 August 2020 / Accepted: 20 March 2021

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Abstract Exotic species can threaten biodiversity by disrupting ecological interactions among native species. Highly-attractive exotic species can exert a ‘magnet effect’ by attracting native pollinators, which may have either competitive or facilitative effects on co-flowering native plants. However, those effects may be context-dependent. We used a mistletoe-hummingbird pollination system in the Valdivian rainforest (southern Chile) to test whether the exotic tree *Eucalyptus globulus* (a highly attractive species to

pollinators) acts as a magnet species, affecting the co-flowering native mistletoe. We compared hummingbird abundance, visitation rates, and activity patterns between native forest and abandoned *E. globulus* plantations. We found that hummingbirds were more abundant and visited more flowers at the plantation irrespective of *E. globulus* flowering. We observed a significant change of pollinator activity at the native habitat during *E. globulus* flowering, as hummingbirds visited mistletoe flowers more frequently early in the morning at the plantations and in the afternoon at the native forests. Our results showed that *E. globulus* acts as an exotic magnet species and can alter pollinator abundance and behavior. Our findings demonstrate the importance of considering local- and landscape-scale processes to understand the effects of magnet species on native plants and suggest that magnet species may influence even highly-attractive plants.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10530-021-02519-2>.

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Keywords Activity kernel · *Eucalyptus globulus* · Temperate rainforest · *Tristerix corymbosus* · *Sephanoides sephaniodes*

Introduction

Increasing human-induced biological invasions are causing biotic homogenization and represent one of the main drivers of biodiversity loss worldwide (Sala

et al. 2000). While not all introduced species become invasive, exotic species introduced outside their ranges—as exotic tree plantations—may modify native communities and affect their structure and functioning (Lewis and Maslin 2015; Vizentin-Bugoni et al. 2019). Exotic species can impact native species in multiple ways, such as reducing species diversity (Vilà et al. 2011) or altering ecological interactions (Simberloff et al. 2013; Traveset and Richardson 2014; Vizentin-Bugoni et al. 2019). However, the indirect effects of exotic species on native communities may be more complex. For instance, exotic plants can be highly attractive to native pollinators allowing their integration into pollination networks and causing changes in the outcomes and dynamics of plant-pollinator interactions between native species (Chittka and Schürkens 2001; Lopezaraiza-Mikel et al. 2007; Aizen et al. 2008).

There has been a long-standing interest in understanding and predicting the effects of ‘magnet species’ on plant-pollinator interactions (Thomson 1978, 1981, 1982; Albrecht et al. 2016; Hegland et al. 2009; Johnson et al. 2003; Laverty 1992; Molina-Montenegro et al. 2008). In general, magnet species produce highly attractive floral resources and disproportionately attract pollinators (Albrecht et al. 2016). Magnet species can have competitive or facilitative effects on co-flowering plants, having a wide range of impacts on the pollination networks depending on the degree of pollinator sharing with other less attractive plants (Johnson et al. 2003; Laverty 1992). Previous studies found that facilitation is more frequent than competition (Hegland et al. 2009; Johnson et al. 2003) even when the magnet species is exotic (Molina-Montenegro et al. 2008; Nielsen et al. 2008). At the local scale, facilitation occurs via positive neighborhood effects (Bruckman and Campbell 2014), when a highly attractive and abundant plant attracts more pollinators and indirectly increases visitation rates and fruit set of less attractive or rare species (Johnson et al. 2003; Laverty 1992). Therefore, facilitation interactions between a magnet species and rare or little attractive co-flowering plants are common and important (Molina-Montenegro et al. 2008; Carvalheiro et al. 2014; Jakobsson et al. 2009), but the effect of magnet species on highly attractive native species remains poorly understood.

Further, there is an increasing consensus that magnet species effects may occur at both small (local

and large (i.e., landscape-scale) spatial scales (Lopezaraiza-Mikel et al. 2007; Jakobsson et al. 2009; Johnson et al. 2003). At the landscape scale, the flowering neighborhood is of paramount importance for pollinator abundance and visitation rates (Fontúrbel et al. 2017a; Bruckman and Campbell 2014). Although neighborhood effects have been studied for a mixture of native and exotic plant species, they have been mostly focused on the facilitation effects of exotic plants on other less attractive native generalist plants (e.g., Molina-Montenegro et al. 2008; Nielsen et al. 2008). On the other hand, the effects of exotic species on abundant native plants are quite common and usually indicate that natives experience reduced reproductive success due to inter-specific competition for pollination services (Morales and Traveset 2009; Montero-Castaño and Vilà 2012). However, the effects of exotic species on pollination interactions are not consistent among studies as they depend on multiple confounding factors, such as plant spatial arrangement and flowering neighborhood (Charlebois and Sargent 2017).

The effects of magnet species form a competition-facilitation continuum, in which we may expect that highly attractive and specialist plant species (i.e., dependent on one or few pollinators) would be negatively affected by the establishment of highly attractive but more generalist co-flowering exotic species. Thus, two highly-attractive and rewarding flowering species (one native and one exotic) are expected to compete for pollinators. This could be even more critical when the pollinators involved exhibit territorial behavior, defending small patches of highly profitable resources, and aggressively displacing other visitors, as is often the case of hummingbirds (in opposition to insect pollinators; Krauss et al. 2017). However, no study has assessed if a magnet-species effect occurs between two highly-attractive plant species to the best of our knowledge. Such effects may be mediated by changes in pollinator behavior, an issue that remains virtually unknown. This may be important because, for example, if exotic magnet species are visited earlier by pollinators, it may cause satiation and therefore decrease visits on native plants and increase pollen limitation and deposition of heterospecific pollen.

Here we studied a pollination system composed of a winter-flowering mistletoe and a generalist hummingbird (Aizen 2003) that coexist with exotic *Eucalyptus*

globulus trees in abandoned forestry plantations (Fontúrbel et al. 2015). The mistletoe and the exotic tree are highly attractive nectar sources to hummingbirds. Their flowering overlaps for about two months—at the end of mistletoe flowering and the beginning of *E. globulus* flowering periods. Aiming to test whether *E. globulus* acts as a potential magnet species affecting pollinator abundance, daily activity patterns, and visitation rates on a native mistletoe, we compared areas with and without *E. globulus*, before and during its flowering period. We hypothesized that: (1) hummingbird abundance will increase in areas with *E. globulus* when it is flowering while hummingbird abundance will decrease in native habitats; (2) hummingbird visitation rates will increase in areas with *E. globulus* during its flowering; (3) hummingbird daily activity patterns between habitats will change during *E. globulus* flowering with hummingbirds being less active (i.e., visiting mistletoe less often) early in the day because they will preferentially use *E. globulus* (i.e., the potential magnet species) flowers instead.

Materials and methods

Study area

We conducted this study at the Valdivian Coastal Reserve (39°57'S, 73°34'W) from August 2017 to October 2017. This private reserve is owned and managed by The Nature Conservancy and protects the largest remnant (~ 50,000 ha) of temperate evergreen rainforests in southern Chile. The Valdivian Coastal Reserve encompasses a mosaic of habitats composed of native forest stands and abandoned *Eucalyptus globulus* plantations (planted 20–25 years ago, not managed, and never harvested). Native forest stands are dominated by *Nothofagus dombeyi*, *Nothofagus pumilio*, and *Eucryphia cordifolia* as canopy trees, and *Laurelia philippiana*, *Drimys winteri*, *Lomatia ferruginea*, and *Mitraria coccinea* in the understory (Fontúrbel et al. 2017a). On the other hand, the abandoned plantations have *E. globulus* as the only canopy tree, and *Ugni molinae*, *Luma apiculata*, *Aristolelia chilensis*, and *Rhaphithamnus spinosus* in the understory (Fontúrbel et al. 2017a).

Habitat characterization

As we compare data from two habitats (i.e., native forests and abandoned *E. globulus* plantations), we first tested whether they differed in structure and abiotic factors. We defined 50 sampling points (24 at the native forest and 26 at the plantation) associated with mistletoe plants. We visually estimated seven variables in the field within a 2.5-m radius from each point: shrub cover (%), bamboo (*Chusquea quila*) cover (%), stem density (number of stems with DBH \geq 1 cm), woody debris (number of snags and fallen logs), temperature (°C, measured in situ with a handheld digital thermometer), relative humidity (%), measured in situ with a handheld digital hygrometer), and luminosity (lux, measured in situ with an LX-1020BS handheld digital luxmeter). We selected those variables to describe habitat differences based on a previous study, which found them relevant to hummingbird visitation rates (Fontúrbel et al. 2017a).

Study species

The hemiparasitic mistletoe *Tristerix corymbosus* (Loranthaceae) is a common species of the South American temperate rainforests. This mistletoe is considered a keystone species due to its flowering phenology (March to October), as it constitutes almost the only nectar source during the austral winter (Aizen 2003). Each flower secretes around 5 μ l of nectar per day, with a w/w sugar concentration of 23% (flowers last 3–4 months; Smith-Ramírez 1993). *Tristerix corymbosus* is self-compatible and almost exclusively pollinated by the hummingbird *Sephaniodes sephaniodes* (Trochilidae) and occasionally visited by bees (Aizen 2005). On the other hand, *S. sephaniodes* is the main vertebrate pollinator in these forests, responsible for pollinating at least 15 native plant species (Smith-Ramírez 1993; Aizen and Ezcurra 1998; Aizen et al. 2002). Resident populations of *S. sephaniodes* depend on *T. corymbosus* flowers as their primary nectar source during the winter, stressing the importance of this interaction at the community-level.

Eucalyptus globulus is native to Australia, and it was introduced in many countries around the world for timber. This species was extensively planted in southern Chile, replacing thousands of hectares of native forests (Echeverría et al. 2006). This perennial tree can grow up to 50 m in height and produce flowers

between September and December (Löewe et al. 1996). *Eucalyptus globulus* has flowers that are white and brush-like, producing 37–56 mg of nectar per day, and a daily volume of up to 300 μ l per flower, with a w/w sugar concentration of 23.4% (Calviño-Cancela and Neumann 2015; Hingston 2002). Given that its nectar production is considerably higher than any other native plant species (Antunes 2003; Hingston 2002; Chalcoff et al. 2006), *E. globulus* represents an attractive resource for both hummingbirds and bees and, thus, it has the potential to act as a magnet species.

Study design and sampling

At the Valdivian Coastal Reserve, we sampled two sites of native forest (i.e., without *E. globulus*; N1 and N2) and two sites of abandoned *E. globulus* plantations (E1 and E2), which were 2–3 km away from each other (Fig. S1, available online as Supporting Information). Mistletoe abundance was similar among sites: N1 = 13.68 ind/ha, N2 = 15.32 ind/ha, E1: 11.83 ind/ha, and E2 = 19.23 ind/ha. Those sites were assessed for three months, divided into two periods (before and during *E. globulus* flowering): August–September and September–October, respectively. To estimate relative hummingbird abundances, we randomly selected six counting points at each sampling site that were sampled before and during *E. globulus* flowering, making 24 points at the native forest and 24 points at the abandoned plantation (12 before and 12 during *E. globulus* flowering). Between 8:00 and 10:00 am, we counted all hummingbirds seen or heard within a 10-min interval (Jiménez 2000; Vizentin-Bugoni et al. 2017).

To quantify *S. sephaniodes* visitation rates and activity, we installed 36 infrared camera-traps (Browning Strike Force HD Pro), 18 at the native forest, and 18 at the abandoned plantation (i.e., nine cameras per sampling site) habitats. Each camera trap was installed in front of a *T. corymbosus* individual, being careful to select individuals of similar size and number of flowers (355 \pm 87 flowers per mistletoe at the native forest, and 286 \pm 48 flowers per mistletoe at the abandoned plantation) and keeping a minimum distance of 50 m among individuals. We georeferenced all focal mistletoes using a GPS device (Garmin GPSMap 62 s; error \leq 5 m). We set camera traps in video mode, operating for 15 s and an inactivity interval of 1 min between shots. From all the video

records obtained, we kept only those that represented effective visits (i.e., with physical contact between the hummingbird and at least one flower) to obtain more realistic estimations of visitation rates. We counted visits at the mistletoe level (i.e., an individual-based approach), considering a visit as each visitation event to the plant, regardless of the number of individuals flowers contacted by the hummingbird.

Statistical analyses

We used a Principal Component Analysis (PCA) to visualize differences between habitats using the seven variables measured in the field. Then, we conducted a Multivariate Analysis of Variance (MANOVA) to assess statistical differences and performed individual ANOVA tests on each variable to determine individually the significance of each habitat variable measured. As mistletoes are usually clumped, they may be influenced by spatial autocorrelation. We examined spatial autocorrelation on the number of flowers and visitation rates using Moran's correlograms with nine distance classes (defined with an equal number of observations per class) ranging from 0 to 4966 m (Table S1). We assessed the significance of each distance class using a bootstrap procedure with 1000 iterations for each case.

We used a Generalized Linear Model (GLM hereafter) with a negative binomial error distribution (to account for overdispersion in the data) and a log link function to compare hummingbird abundance between native forest and abandoned plantation habitats, as well as between before and during *E. globulus* flowering. We fitted a GLM to compare hummingbird visitation rates between habitats and periods, including the number of *T. corymbosus* flowers as a covariate, as it may affect each individual's display and its attractivity to pollinators. Because we detected spatial autocorrelation for hummingbird visits between 32 and 214 m (Table S1), we also examined spatial autocorrelation on the residuals of the GLM model to test if our results are affected by spatial structure, using partial Mantel correlograms. We used the packages 'mgcv' (Wood and Scheipl 2014), 'lme4' (Bates et al. 2013), 'AER' (Kleiber and Zeileis 2008), and 'ncf' (Bjornstad 2013) for model fitting, the package 'mpmcorrelogram' (Matesanz et al. 2011) to examine spatial autocorrelation, the packages 'vegan' (Oksanen et al. 2013), ade4 (Dray and Dufour 2007)

and ‘factoextra’ (Kassambara and Mundt 2020) to perform PCA analyses, and the packages ‘ggplot2’ (Wickham 2016) and ‘plotrix’ (Lemon 2006) for graphics. We conducted all analyses in R 3.6.1 (R Development Core Team 2019).

To assess *S. sephaniodes* activity patterns, we first filtered raw camera trap data (i.e., all hummingbird records) using 30-min intervals to increase the observations’ independence (i.e., to reduce the chance of counting the same individual more than once and avoid pseudoreplication). With the filtered dataset, we estimated activity kernels for each habitat type and flowering period. An activity kernel is a density function that estimates how much activity is concentrated at different times throughout the day. Then, we compare activity kernels between areas and periods using the $\hat{\Delta}_4$ overlapping coefficient, as recommended by Ridout and Linkie (2009). We then used a randomization procedure (1000 bootstraps) to test if the observed activity patterns differ from the random expectation. We performed activity analyses using the R packages ‘circular’ (Ridout and Linkie 2009) and ‘activity’ (Rowcliffe 2019).

Data availability

Original data is available from the *figshare* digital repository: <https://doi.org/10.6084/m9.figshare.12058890>

Results

We found that habitat structure differed between the native forests and the abandoned plantations (MANOVA $F_{7,42} = 2.37$, $P = 0.039$; Fig. S2). Structural differences between these habitats were explained by significant variations in woody debris and luminosity (Table S2). While woody debris is scarce in the abandoned plantations, there is more light incidence as *E. globulus* trees form an opener canopy allowing more sunlight to reach the understory.

Before *E. globulus* starts its flowering period, we recorded 5.33 ± 0.91 (mean \pm 1SE) hummingbirds per census point (64 individuals in total) at the native forest and 10.83 ± 2.31 hummingbirds at the abandoned plantation (103 individuals in total). In contrast, when we repeated hummingbird censuses during *E.*

globulus flowering, we recorded 8.50 ± 0.74 hummingbirds (102 individuals in total) at the native forest and 17.25 ± 1.96 hummingbirds (207 individuals in total) at the abandoned plantation. We found significant effects of habitat type (GLM estimate = -0.708 , SE = 0.164, $P < 0.001$) and flowering period on hummingbird abundance (Fig. 1a; GLM estimate = 0.466, SE = 0.164, $P < 0.001$), as hummingbirds were more abundant at the abandoned plantation, but the number of hummingbirds increased in both habitats when *E. globulus* was flowering. Likewise, before *E. globulus* flowering, we recorded

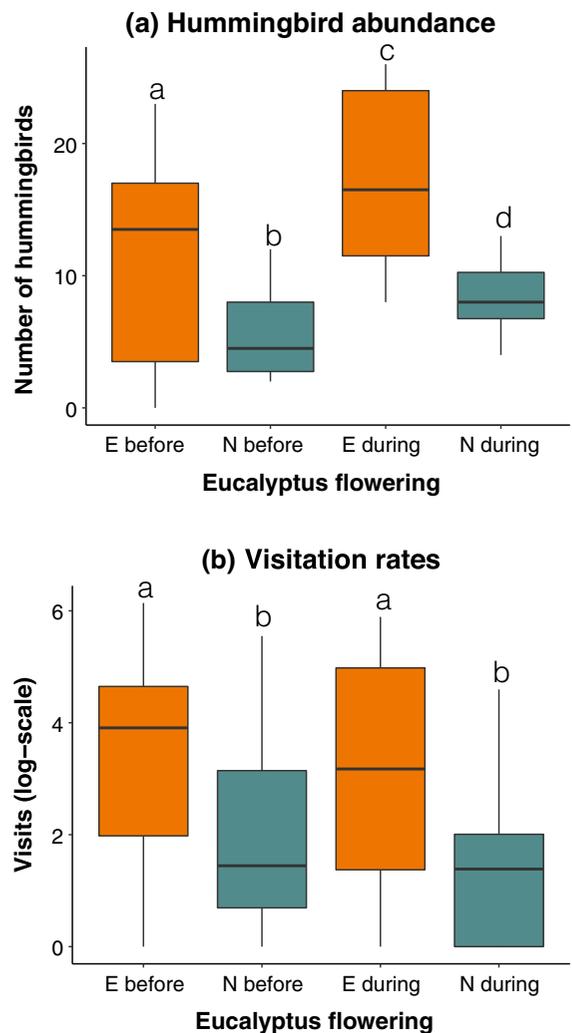


Fig. 1 Differences in **a** hummingbird abundance and **b** visitation rates on *Tristerix corymbosus* flowers between habitats (N = native forest and E = *Eucalyptus globulus* plantation) and *E. globulus* flowering periods (before and during). Different letters indicate significant differences across comparisons

582 effective visits to *T. corymbosus* flowers at the native forest (33.44 ± 15.74 visits per plant) and 1777 visits at the abandoned plantation (100.50 ± 33.79 visits per plant), while during *E. globulus* flowering, we recorded 262 effective visits at the native forest (13.44 ± 6.77 visits per plant) and 1546 visits at the abandoned plantation (89.89 ± 25.81 visits per plant). In this case, we found that visitation rates were higher at the plantation habitat regardless whether *E. globulus* was flowering or not (GLM estimate = -1.518 , SE = 0.408 , $P < 0.001$), and that visitation rates tended to reduce in both habitats during *E. globulus* flowering, but differences were not statistically significant (Fig. 1b; GLM estimate = -0.571 , SE = 0.408 , $P = 0.162$). Further, the number of flowers (included as a covariate in the analyses) showed no effect (GLM estimate = 0.001 , SE = 0.001 , $P = 0.156$). We found no spatial autocorrelation in the GLM residuals (Fig. S3); consequently, our visitation results were not influenced by the mistletoe spatial structure. Detailed GLM results are available in Tables S3 and S4.

When we assessed pollinator daily activity patterns, we found that *S. sephaniodes* activity started at 06:00 and ended at 18:00, being variable between habitats and *E. globulus* flowering periods (Fig. 2). Comparing activity patterns at each habitat before and during *E. globulus* flowering, we observed significant changes at both the native forest (Fig. 2a; $\hat{\Delta}_4 = 0.891$, $P = 0.005$) and the abandoned plantation (Fig. 2b; $\hat{\Delta}_4 = 0.929$, $P < 0.001$), but the change was more pronounced at the native forest. Specifically, activity kernels for both native forest and abandoned plantation habitats were similar before *E. globulus* flowering (Fig. 2c; $\hat{\Delta}_4 = 0.945$, $P = 0.114$), but changed significantly during *E. globulus* flowering at the native forest (Fig. 2d; $\hat{\Delta}_4 = 0.906$, $P = 0.010$), where most of the activity was concentrated in the afternoon while most of the activity at the abandoned plantation was concentrated in the morning. Hummingbird records were larger at the abandoned plantation at both flowering periods (Fig. 3).

Discussion

Our results showed that a highly-attractive exotic species, *Eucalyptus globulus*, act as a magnet species

and can alter pollinator abundances, visitation rates, and activity patterns of a highly-attractive co-flowering native species. In this particular case, the native mistletoe *Tristerix corymbosus* is highly-attractive for hummingbirds, being almost the only native nectar source available during the austral winter (Aizen 2003). *Tristerix corymbosus* winter-flowering phenology allows it to monopolize most of the pollination services that hummingbirds provide (Aizen 2003), but, in the presence of *E. globulus*, the mistletoe has to share such pollinators with the exotic tree.

In this novel ecological scenario, hummingbird abundance increased in both habitats during *E. globulus* flowering, but hummingbirds were more abundant at the abandoned plantations regardless of *E. globulus* flowering. This outcome suggests that hummingbirds are attracted to the abandoned plantations for additional reasons than *E. globulus* floral resources. Such reasons may include a higher density of mistletoes (Fontúrbel et al. 2015, 2017b), which may attract more hummingbirds to those habitats due to the large floral displays and resource availability, but may also be related to predator avoidance and more amenable conditions (i.e., warmer temperatures, fewer winds), which requires further investigation. Altogether, we detected differences in habitat structure between native forest and abandoned plantations. Like most hummingbirds, *S. sephaniodes* is capable of memorizing plant locations and nectar replenishing times as well as to defend territories (González-Gómez and Vásquez 2006; González-Gómez et al. 2011, 2015; Justino et al. 2012). Consequently, *S. sephaniodes* individuals may be highly capable of adjusting their distribution, feeding patterns, and territories in the landscape in response to increased resource availability due to *E. globulus* flowering, as our results indicated. Accordingly, mistletoes at both habitats tended to receive fewer visits when *E. globulus* was flowering, but those differences were not statistically significant.

We also observed higher visitation rates on the mistletoe at the abandoned plantations than in native habitats, irrespectively of *E. globulus* flowering. We initially expected visitation rates to be similar between habitats before *E. globulus* flowering but to increase at the abandoned plantation and reduce at the native forest during *E. globulus* flowering. This was not confirmed by our results, which indicated that hummingbirds are attracted to the region from more distant

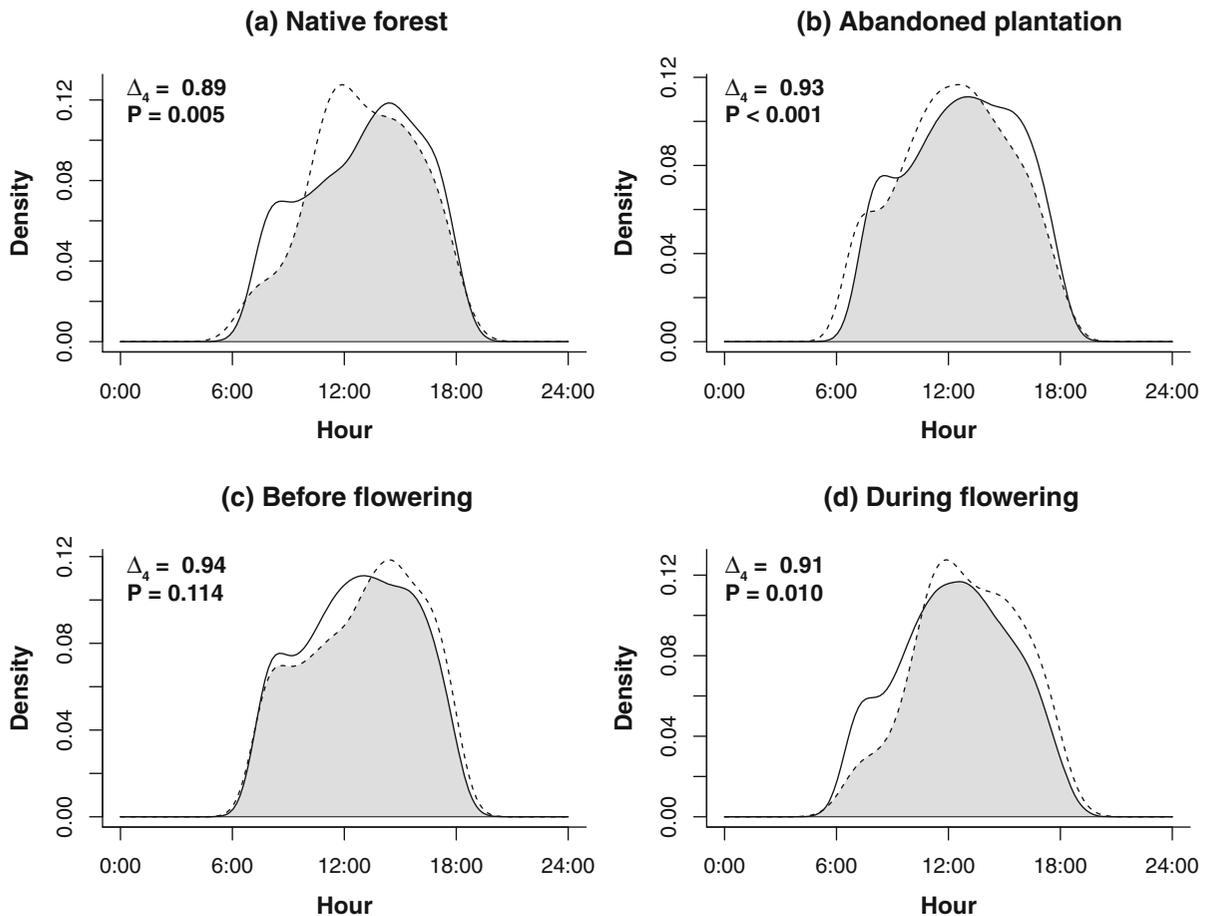


Fig. 2 *Sephanoides sephaniodes* activity kernel density functions for native forest (a) and abandoned plantation (b) habitats, and for before (c) and during (d) *Eucalyptus globulus* flowering period. Upper panels: the continuous line represents the period before *Eucalyptus globulus* flowering, and the dashed line represents the period during *E. globulus* flowering. Lower

panels: the dashed line represents the native forest habitat, and the continuous line represents the abandoned plantation habitat. Gray areas represent the overlapping between both density kernel curves. We present Δ_4 estimators and P-values for each comparison

areas, increasing its regional population density. Interestingly, this may not necessarily translate into facilitation for *T. corymbosus* specifically, since it has a single ovule per flower and is self-compatible (Aizen 2005). Thus, a single visit may be sufficient for this mistletoe to set the maximum number of seeds per flower (one seed) even with the delivery of a single pollen grain from the same individual plant. Usually, facilitation effects involving magnet species are associated with inconspicuous plant species rarely visited by pollinators (Molina-Montenegro et al. 2008; Nielsen et al. 2008). Nonetheless, in this case, a similar outcome for a highly abundant and attractive native mistletoe and an exotic tree would be expected, which

does not translate into facilitation because of the system's intrinsic characteristics (i.e., a single ovule and self-compatibility).

We also found that hummingbird activity changes over time at the landscape scale. During *E. globulus* flowering, *S. sephaniodes* changed their activity pattern at the native forest habitat, concentrating their activity after the activity peak at the plantations. Furthermore, *T. corymbosus* genetic flow patterns previously reported in the study area show high inbreeding rates in the abandoned plantations and asymmetric gene flows between native forests and plantations, resulting in a reduced genetic diversity in the plantations (Fontúrbel et al. 2019). This may be a

Arriaga 2016), ultimately determining the genetic diversity of the mistletoe offspring.

Synthesis and application

Exotic plant species can be integrated into plant-pollinator networks, altering their structure and pollination effectiveness (Memmott and Waser 2002; Carneiro et al. 2008). Particularly, highly abundant and attractive exotic plants can attract many native pollinators, expediting their integration into the native community. The so-called magnet species can either pose facilitation or competitive effects on the co-flowering native plants. In particular, we showed that *E. globulus* act as a magnet species influencing hummingbird abundances and behavior. *Eucalyptus globulus* presented a potential for facilitation effects on a highly-attractive and abundant native mistletoe, which were not realized due to its intrinsic characteristics. This study highlights the complexity behind exotic magnet species, which may have contrasting effects on pollination interactions at different scales. These findings are relevant for conservation practice and habitat management. The establishment of large monocultures of highly-attractive exotic species can indirectly alter the outcome of pollination interactions beyond their boundaries, affecting the neighboring native vegetation remnants.

Acknowledgements We are grateful to The Nature Conservancy and the Valdivian Coastal Reserve staff for authorizing the fieldwork and giving us access to facilities to conduct this study. C. Valenzuela assisted in the fieldwork. R.A. Dias provided valuable suggestions to the methodology. Comments of C. Botto, D. Véliz, R. Vásquez, and three anonymous reviewers improved an early version of this manuscript. This study was conducted with the funding of Fondo Nacional de Desarrollo Científico y Tecnológico (FONDECYT, Chile), project 11160152 (to FEF). JVB thanks CERL-ERDC and CAPES for financial support.

Authors' contribution J.V.B. and F.E.F. conceived the ideas and designed the methodology. J.C.V. and F.E.F. collected field data. J.C.V. processed field data. J.C.V. and F.E.F. analyzed data with contributions of J.V.B. F.E.F. led manuscript writing with contributions of J.C.V. and J.V.B.

Funding This research was funded by Fondo Nacional de Desarrollo Científico y Tecnológico (FONDECYT, Chile), grant 11160152 to FEF. CERL-ERDC and CAPES (Finance code 001) financially supported JVB.

Availability of data and material Figshare digital repository: <https://doi.org/10.6084/m9.figshare.12058890>.

Declarations

Conflict of interest All authors declare no conflict of interest.

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