

Invader complexes or generalist interactions? Seasonal effects of a disturbance gradient on plants and floral visitors

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ABSTRACT

Disturbances can facilitate the spread of exotic plants, which establish mutualisms with exotic bees, constituting invader complexes. However, a disturbance-mediated increase in flower resources can also promote native floral visitors due to the fact that plant-pollinator interactions are generalist. We experimentally tested these ideas in northern Patagonian woodlands. In three sites, we examined the effect of harvesting intensity (HI) (0%, 30%, 50%, 70% of biomass removal) on flower density (exotic: herbs; native: herbs, shrubs, trees) and floral visitor density (exotic: honey bees, bumblebees; native: bees and wasps, hoverflies, other flies, beetles, ants). For four years, we made observations throughout the flowering period to test seasonality. HI had the most substantial positive effect on native herbs, followed by shrubs, and it was null on trees. The effects on the floral density of exotic herbs depended on site. HI enhanced the density of exotic bumblebees, native bees and wasps, and hoverflies; but it had no effect on honey bees, and it showed variable effects on the other floral-visitor groups. Although seasonality was relevant, there was no strong interaction with HI. In general, HI enhanced the density of native and exotic floral visitors, which is better explained by generalist interactions rather than by invader complexes.

1. Introduction

Exotic species can interact and mutually benefit, creating what is known as “invader complexes” (D’Antonio and Dudley, 1993). In plant-pollinator interactions, it has been reported that some invasive bees are more likely to interact with exotic plants (Morales and Aizen, 2002, Traveset et al., 2013). Invasive pollinators can compete with other floral visitors, modifying pollination (Aizen et al., 2014); and exotic plants can also compete with native plants and alter ecosystem attributes (Levine et al., 2003). However, the invader complex hypothesis does not always predict the identity of the resource used by invasive bees, because some species indistinctly use native and exotic plants (Morales and Aizen, 2002, Olesen et al., 2002). Many pollinators are generalists, i.e. they forage on many plants (Waser et al., 1996), which is a common attribute in invasive bees like the honey bee and *Bombus* spp. (Aizen et al., 2014).

Disturbances associated with ecosystem management can promote invader complexes. In particular, disturbances that imply biomass removal like logging can increase resource availability, of which exotic

plants take advantage (Davis et al., 2000). As a result, the relative abundance of exotic plants can be greater in disturbed areas compared to less disturbed ones, which can make the former more attractive to invasive bees (Morales and Aizen, 2002). However, disturbances can also promote native flowers that benefit native pollinators (Morales and Aizen, 2002, Korpela et al., 2015). When evaluating management strategies to assess and forecast their potential impacts on plant-pollinator interactions, these complex community responses require addressing disturbances on both native and exotic components.

In addition to disturbances, plant-pollinator interactions are subjected to significant changes throughout the flowering season. This variation is related to turnovers in species composition of both plants and pollinators (Dicks et al., 2002), and plant flowering phenology (Olesen et al., 2008), among other factors. The variation in the aforementioned interactions can lead to varying effects of disturbance throughout the flowering season (Galbraith et al., 2019). Floral resources of exotic plants can be more relevant at the end of the season (Salisbury et al., 2015, Frankie et al., 2019, Staab et al., 2020). In this

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sense, if there is a temporal matching between exotic plants and invasive bees, the establishment of invader complexes promoted by disturbances will be restricted to that period.

Nothofagus antarctica woodlands of northern Patagonia are characterized by a high dependence of many plant species on biotic pollination, which is a more common characteristic in tropical ecosystems than in temperate ones (Aizen and Ezcurra, 1998). Based on the presence of only one native bumblebee *Bombus dahlbomii* that pollinates many plants and the rapid and successful establishment of the exotic bumblebee *Bombus ruderatus*, the existence of “empty bumblebee niches” has been suggested (Roig-Alsina and Aizen, 1996, Aizen and Ezcurra, 1998). In the area, another two more invasive bees are established: *Apis mellifera* and *Bombus terrestris* (Morales and Aizen, 2002, Torretta et al., 2006, Aizen et al., 2014). Currently, there is a growing interest in understanding how to harvest Patagonian woodlands sustainably, yet the effects of management practices on shaping the interactions between exotic and native species are unclear (Coulin et al., 2019, Goldenberg et al., 2020, Nacif et al., 2020). Assessing these issues is mandatory to design more sustainable practices that do not affect native biodiversity, and that control the expansion of exotic species and their potential negative effects.

This study aims to evaluate the effect of woodland harvesting intensity on the floral density of native and exotic plants, and on the density of their native and exotic floral visitors, with emphasis on invasive bees (*Apis mellifera* and *Bombus* spp.). Specifically, it is evaluated whether harvesting intensity as a disturbance promotes an increase in the density of exotic flowers and visitors over their native counterparts, as expected by the hypothesis of invader complexes. Or if on the contrary, both native and exotic pollinators benefit from an increase in floral resources independently from their origin in response to harvesting intensity, as expected by the prevalence of generalist interactions. We also evaluated if the expected patterns vary or remain constant during the flowering season and among contrasting woodland sites.

2. Methods

2.1. Experimental design and sampling

The study was performed at three sites in *Nothofagus antarctica* woodlands of Río Negro, Argentina that correspond to private lands destined to research. Sites differ in biomass productivity (kg/ha.year), plant community composition, and physiognomic structure (Coulin et al., 2019, Goldenberg et al., 2020). The sites Foyel Sur (FS) and Foyel Norte (FN) are located near El Foyel (41° 38' S, 71° 29' W) and correspond to the south and north side of the same hillside, respectively. The third site is located at Los Repollos (R) (S 41° 46', W 71° 28') in a valley bottom. All sites have similar altitudes: 790 m above mean sea level for sites FS and FN and 880 m above mean sea level for site R (Oddi et al., 2021). FS has an annual mean temperature of 7.0 °C, a mean winter temperature of 2.5 °C, and an annual rainfall of 1100 mm. It is the most productive site and the canopy is dominated by *Nothofagus antarctica*, *Diostea juncea*, *Schinus patagonicus*, *Lomatia hirsuta*, and *Embothrium coccineum* (Coulin et al., 2019, Goldenberg et al., 2020). FN has an annual mean temperature of 8.0 °C, an average winter temperature of 2.7 °C and an annual rainfall of 1100 mm. It has intermediate productivity and the canopy is dominated by *N. antarctica*, *S. patagonicus*, *L. hirsuta*, *Fabiana imbricata* and *E. coccineum* (Coulin et al., 2019, Goldenberg et al., 2020). R has an average annual temperature of 9.4 °C, an average winter temperature of 2.3 °C and an annual rainfall of 950 mm. It is the site with the lowest productivity and the canopy is dominated only by *N. antarctica* (Coulin et al., 2019, Goldenberg et al., 2020).

Local legislation establishes that most of the woodlands in the province of Río Negro cannot be replaced by the afforestation of exotic species and must be managed in a sustainable way (Ley Nacional Argentina 26.331 2007). One potential use is the removal of woody biomass for fuelwood (Goldenberg et al., 2020). However, the

comprehensive study of the ecological consequences of this type of activity is incipient.

We delimited eight plots (31.5 × 45.0 m) per site, and we applied four levels of harvesting intensity (hereafter HI), with one repetition. Plots were adjacent or separated by less than 400 m. Treatments differed in the percentage of plant cover removal (0, 30%, 50%, 70%) and were obtained by tracing six strips of the same width according to the treatment in which trees and shrubs were cut at ground level (30%: 1.5 m wide, 50%: 2.5 m wide, 70%: 3.5 m wide, Appendix 1). Branches with a diameter up to 4 cm and leaves were left on the ground. Harvesting treatments were applied only once at early 2013 for FS, early 2014 for FN, and late 2013 for R.

We delimited two circular subplots (4 m radius) per plot for measuring floral density (one placed in the center and another placed randomly every year (Appendix 1). For entomophilous plant species, we registered the number of flowering individuals and the number of floral units per individual in each subplot. Floral units included flowers and capitula (e.g., Asteraceae). We conducted surveys repeatedly every 15–20 days during the main months of the flowering season (November, December and January) in 2014–2015 (year 1), 2015–2016 (year 2), 2017–2018 (year 3) and 2018–2019 (year 4). We surveyed half of each subplot for herbs and shrubs since their density is higher than trees.

For measuring the density of floral visitors, we chose one individual of each flowering species per plot, and we observed all the animals that visited a selected number of floral units during 10 min. During November, December and January of the same four years we conducted censuses on sunny days, between 9:00 and 19:00 h. every week on each site when weather conditions allowed it. Ideally, all plots in one site were surveyed on the same day and the order of the plots was changed each new day. The censuses were repeated on randomly chosen individuals per site and per week until the flowering of the specific plant species ended. The total observation time varied between species, plots, and sites because of differences in the period of flowering, abundance and spatial distribution. We conducted 3858 floral visitor censuses (i.e., 643 h of observation). We classified floral visitors by morphotypes, and we worked with averaged values between years since our focus was on the general response to HI and intra-annual variation. In fact, the inter-annual variation of floral visitor density was low (Appendix 2).

2.2. Response variables

We calculated floral density (No./ha) per plot and month for the different plant groups based on their status and habit (exotic: herbs, native: herbs, shrubs and trees) (Appendix 3). All exotic plants were herbs, except for some individuals so rare that they were highly unlikely to affect pollinator density at the plot level. Since not all the plant species were present in subplots, we combined the censuses of plants and floral visitors. We calculated the average floral density for each species for each month and summed them across all plant groups, and we afterward averaged the values of each year and extrapolated them to the hectare scale.

We calculated the density of floral visitors (No./ha) per plot and month for the different groups (honey bees, exotic bumblebees, native bees and wasps, hoverflies, other flies, beetles and ants). We first multiplied the number of floral visitors per flower (individuals/floral unit) per census by the floral density (floral units/m²) values of the closest floral census in time. We subsequently calculated the average floral visitor density for each morphotype and each month, and we summed them across visitor groups. We then averaged the values of each year and extrapolated them to the hectare scale.

2.3. Statistical analyses

Using mixed-effect models, we tested the effect of HI on the floral density of the plant groups (4 models, Table 1), and the density of floral visitor groups (7 models, Table 2). Fixed effects included the following

Table 1

Influence of M (month), S (site), HI (harvesting intensity) and HI² (squared harvesting intensity) on floral density (Ln No./ha) of exotic herbs, native herbs, native shrubs and native trees. Model estimates and 95% confidence intervals from the model with the lowest AIC are shown. AIC values of the minimum adequate model and the null model, as well as their difference are presented. Estimates are mean values for fixed effects, and variance values for random effects. Abbreviations: FN (Foyel Norte), R (Los Repollos), D (December), J (January). For clarity, triple interactions were removed from the table.

Coefficients	Exotic herbs	Native herbs	Native shrubs	Native trees
Intercept	6.64 (4.18,9.09)	6.89 (5.61,8.17)	14.48 (13.28,15.69)	13.75 (13.18,14.32)
FN	-5.15 (-8.53,-1.76)	-	-0.40 (-1.93,1.14)	-
R	0.08 (-3.26,3.42)	-	-3.60 (-5.13,-2.07)	-
D	-2.10 (-3.44,-0.75)	2.16 (1.07,3.25)	-1.46 (-3.0,0.07)	-
J	-1.15 (-2.50,0.20)	1.75 (0.66,2.84)	-6.27 (-7.81,-4.74)	-
HI	3.17 (-11.87,18.21)	5.71 (3.46,7.95)	1.29 (-0.11,2.68)	-
HI ²	-4.45 (-25.62,16.73)	-	-	-
FN:D	-	-	0.73 (-1.44,2.89)	-
R:D	-	-	-4.60 (-6.77,-2.43)	-
FN:J	-	-	4.74 (2.57,6.91)	-
R:J	-	-	7.58 (5.41,9.75)	-
FN:HI	25.31 (3.59,47.03)	-	-	-
R:HI	-6.98 (-28.32,14.36)	-	-	-
D:HI	-	-	-	-
J:HI	-	-	-	-
FN:HI ²	-38.04 (-68.51,-7.57)	-	-	-
R:HI ²	17.92 (-11.14,46.97)	-	-	-
D:HI ²	-	-	-	-
J:HI ²	-	-	-	-
Random intercepts	1.25	1.14	3.49e-09	0.97
Residual variance	5.66	3.72	2.45	0.88
AIC minimum adequate model	365.92	324.38	292.78	110.48
AIC null model	395.47	351.20	384.95	110.48
ΔAIC(null-minimum)	29.55	26.82	92.17	0.00

variables: site (S, qualitative), month (M, qualitative), harvesting intensity (HI, quantitative) and squared harvesting intensity (HI², quantitative) to account for non-linear effects. Two-way and three-way interactions were included, and the plot was considered as a random effect. Models were estimated using the package glmmTMB (Brooks et al., 2017) in R software (R Core Team 2021) and fitted with a Gaussian distribution. Based on multimodel inference, we selected the best fitting models using the Akaike Information Criterion and the dredge function from the package MuMin (Burnham et al., 2011). For figures, we only presented those selected models whose AIC values differ by more than 6 compared to the null models. We also calculated the relative importance of each predictor with the importance function from the package MuMin. Before the analyses, both flower and floral visitor densities values were log-transformed (ln).

Spearman correlation analysis was conducted between the floral

density of plant groups and the density of floral visitor groups by using the rcorr-function of the Hmisc package (Harrell, 2021) in R software (R Core Team 2021).

3. Results

3.1. Effects of harvesting intensity on floral density

All models included information from the three sites and the three months, except the model for native trees. In the latter, the information from site R was not included because this woodland type had a very low density of flowering trees (Appendix 4). January data from site FS and FN was also not included because the flowering period of trees ends mainly at the end of December (Appendix 4). This removal made it possible to considerably increase the goodness-of-fit of the native tree model.

A clear positive effect of harvesting was found on the floral density of native herbs, a positive trend but of less magnitude in native shrubs, a null effect on native trees and a site-dependent effect on exotic herbs. In all cases, the difference between the AIC values of the best-fitting model with the null model was always greater than 6, except for native trees where the null model had the lowest AIC value (Table 1). The selection of predictors by the best-fitting model for each plant group (Table 1) agreed with the results of relative importance analysis (Appendix 5). The best-fitting model for exotic herbs included HI and HI² and their interaction with site (Table 1). The model showed contrasting effects according to site conditions: a clear effect in site FN, an apparent increase in site R and null effect in site FS (Table 1, Fig. 1). HI was included in the best-fitting models for native herbs and shrubs but the effect was stronger in the former (Table 1, Fig. 1). Although site was included in the native herb model, and month and site in the native shrub model, there was no interaction between these variables and HI (Table 1).

3.2. Effects of harvesting intensity on floral visitor density

All models included information from the three sites and the three months, except for the exotic bumblebee model. Information from site R was not included as the density of this group is extremely low on this site (Appendix 4). This made it possible to considerably increase the goodness-of-fit of the exotic bumblebee model.

Harvesting intensity had a positive effect on the density of exotic bumblebees, native bees and wasps group and hoverflies but a null effect on honey bees. The effect on ants was site-dependent, while on other flies and beetles was both site- and month-dependent. In all cases, the difference between the AIC values of the best-fitting model with the null model was always greater than 6, except for honey bees where the null model had the lowest AIC value (Table 2). The selection of predictors by the best-fitting model for each floral visitor group (Table 2) agreed with the results of relative importance analysis (Appendix 5). HI was included in the model for exotic bumblebees, native bees and wasps and hoverflies and its effect was independent of month and site (Table 2, Fig. 2). Both HI and HI² and their interaction with month and site were included in the models for other flies and beetles (Table 2). In general, the effect on other flies reached a peak at 50% harvesting intensity at site FS, at 30% at site FN, and two peaks at 0% and 70% at site R (Fig. 2). The effect on beetles usually peaked at high intensities (70%), particularly in November at site R and January at site FS (Fig. 2). For ants, HI and its interaction with site were included on the best fitting model and the effect of harvesting was positive on sites FS and R and negative at site FN (Table 2, Fig. 2).

3.3. Relation between flower density and floral visitor density

In general, the density of floral visitors was positively correlated with the floral density of the native plant groups. Spearman's correlation analysis showed a significant positive relationship between the floral

Table 2

Influence of M (month), S (site), HI (harvesting intensity) and HI² (squared harvesting intensity) on the density (Ln No./ha) of honey bees, exotic bumblebees, native bees and wasps, hoverflies, other flies, beetles and ants. Model estimates and 95% confidence intervals from the model with the lowest AIC are shown. AIC values of the minimum adequate model and the null model, as well as their difference are presented. Estimates are mean values for fixed effects and variance values for random effects. Abbreviations: FN (Foyel Norte), R (Los Repollos), D (December), J (January), NE (not evaluated). (*) for the model for ants, the residual variance was modeled by month and site. For clarity, triple interactions were removed from the table.

Coefficients	Honey bees	Exotic bumblebees	Native bees and wasps	Hoverflies	Other flies	Beetles	Ants
Intercept	1.59 (1.18,2.01)	0.77 (-0.39,1.92)	6.79 (5.64,7.93)	1.97 (0.64,3.29)	4.38 (3.22,5.54)	2.11 (0.89,3.33)	3.54 (2.02,5.06)
FN	-	-0.39 (-1.76,0.98)	-1.43 (-2.88,0.03)	-0.02 (-1.71,1.66)	0.21 (-1.18,1.61)	3.52 (1.85,5.20)	0.64 (-1.75,3.04)
R	-	-	-6.21 (-7.66,-4.75)	-1.73 (-3.41,-0.04)	-0.46 (-1.86,0.94)	-1.69 (-3.33,-0.04)	-3.13 (-5.00,-1.25)
D	-	0.95 (-0.36,2.26)	-1.53 (-2.99,-0.07)	0.36 (-1.33,2.04)	-1.58 (-2.64,-0.53)	2.62 (1.04,4.21)	-3.12 (-4.44,-1.80)
J	-	0.63 (-0.68,1.94)	-2.92 (-4.37,-1.46)	-0.61 (-2.29,1.08)	-0.71 (-1.76,0.35)	-1.32 (-2.91,0.26)	-3.07 (-4.44,1.70)
HI	-	2.21 (0.54,3.87)	1.81 (0.48,3.14)	1.63 (0.09,3.16)	6.42 (-0.07,12.91)	-2.35 (-6.18,1.48)	0.72 (-1.62,3.06)
HI ²	-	-	-	-	-10.55 (-19.83,-1.27)	3.58 (-3.23,10.38)	-
FN:D	-	-1.70 (-3.54,-0.16)	0.35 (-1.71,2.41)	-1.67 (-4.06,0.71)	-	-3.03 (-5.28,-0.79)	1.21 (-1.25,3.68)
R:D	-	-	2.86 (0.80,4.92)	-0.19 (-2.57,2.19)	-	0.68 (-1.57,2.93)	2.59 (-0.76,4.41)
FN:J	-	1.46 (-0.39,3.31)	1.22 (-0.84,3.28)	2.30 (-0.09,4.68)	-	1.07 (-1.18,3.31)	0.22 (-1.96,2.39)
R:J	-	-	6.07 (4.01,8.13)	3.18 (0.79,5.56)	-	5.41 (3.16,7.65)	4.00 (2.31,5.69)
FN:HI	-	-	-	-	0.72 (-8.45,9.90)	-	-3.12 (-6.32,-0.08)
R:HI	-	-	-	-	-15.02 (-24.19,-5.85)	-	2.59 (-0.88,6.06)
D:HI	-	-	-	-	-	-	-
J:HI	-	-	-	-	-	-	-
FN:HI ²	-	-	-	-	-4.05 (-16.80,8.70)	2.24 (-3.78,8.26)	-
R:HI ²	-	-	-	-	18.86 (6.10,31.61)	11.70 (5.61,17.78)	-
D:HI ²	-	-	-	-	3.65 (-0.15,7.44)	0.63 (-5.07,6.33)	-
J:HI ²	-	-	-	-	6.22 (2.42,10.01)	14.93 (9.23,20.62)	-
Randomintercepts	3.95 e-9	0.18	5.97e-10	3.24e-09	1.92e-10	0.14	0.64
Residualvariance	3.29	1.78	2.21	2.61	1.56	1.17	NE (*)
AIC minimumadequate model	296.1	186.22	285.46	306.38	266.16	264.63	289.95
AIC null model	296.1	197.03	332.81	315.45	298.67	317.34	316.26
ΔAIC(null-minimum)	0.00	10.81	47.35	9.07	32.51	52.71	26.31

density of native herbs and the density of hoverflies and beetles ($P \leq 0.05$), but marginally significant with the density of exotic bumblebees ($P = 0.05-0.1$) (Table 3). It also showed a significant positive correlation between the floral density of native shrubs and the density of honey bees, native bees and wasps, hoverflies, other flies and ants; and between the floral density of trees and the density of the group of native bees and wasps and ants (Table 3). A negative relationship was found between the floral density of exotic herbs and the density of beetles (significant, $P \leq 0.05$) and between the floral density of native herbs and the density of ants (marginally significant, $P = 0.05-0.1$) (Table 3).

4. Discussion

Our results showed that HI had a notably positive effect on the floral density of native herbs and a positive trend on native shrubs, but a variable effect on the floral density of exotic plants. Overall, HI also enhanced the density of both native and exotic floral visitors. Generally, floral visitor density was positively related to the floral density of native plant groups. As expected, seasonality was an important variable explaining the variation of flower and floral visitor densities. However, HI was independent of seasonality in most cases. Particularly, the effect on exotic bumblebees, native bees and wasps, and hoverflies was positive across the flowering season and sites.

The results of the present study show that the response of native floral density to HI can be ordered according to plant habit, from very strong in the case of herbs, with a positive trend in shrubs, and absent (i. e., no effect) in trees. The stronger response of native herbs is due to the fact that most woodland species are limited by light (Whigham, 2004). Shrubs, on the other hand, are less limited by light, although some smaller species probably benefit from the gaps generated (Agüero, pers. obs.). The effect of HI on tree floral density can be null if standing individuals increase the number of flowers (Herrerías-Diego et al., 2006). Only the effect on exotic herbs was site-dependent, which may be related to the history of use. The most substantial response was found in site R, which had a strong history of disturbance, especially of livestock, that could facilitate seed dispersal (Whigham, 2004). For the same sites and in the first two years of the present experiment, the impact of HI on total floral density (considering all groups) was variable, and depended on site and year (Coulin et al., 2019). However, in a long-term study, logging consistently increased total floral abundance in boreal forests (Pengelly and Cartar, 2010). Other studies also found a positive impact on the abundance of flowering plants (Romey et al., 2007) and flower coverage (Korpela et al., 2015). Seasonality (i.e., sampled month) explained most of the variation in native herbs and native shrubs floral density. However, the HI effect was independent of it. The only other study that evaluated a similar idea was carried out in a managed mixed-

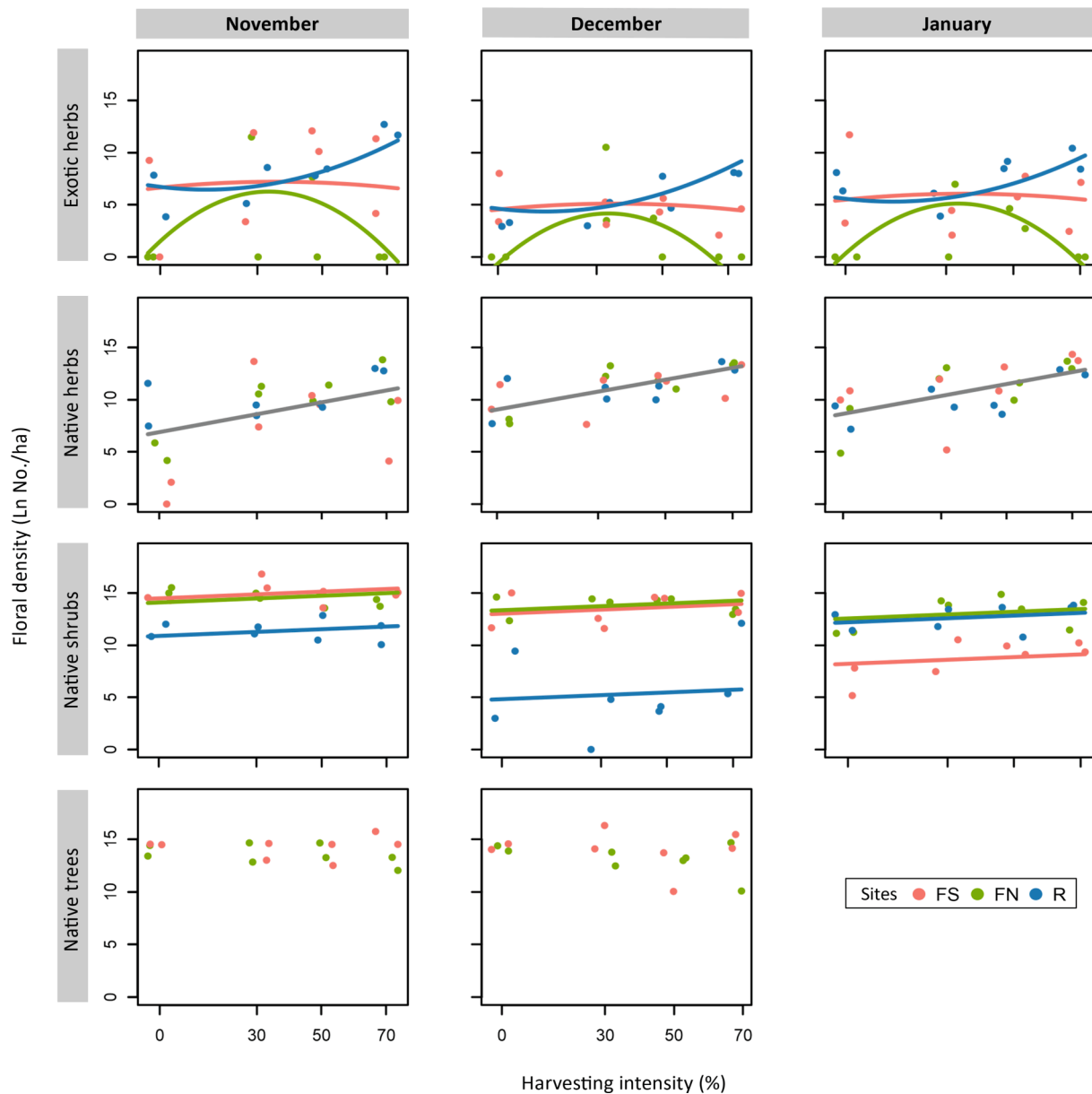


Fig. 1. Effect of harvesting intensity (HI) on the floral density of plant groups for the main flowering months and for each site. Dots correspond to the average value of a plot, and curves represent the predicted values from mixed-effect models. Curves are absent if HI is not included in the minimum adequate model selected by AIC (Akaike Information Criteria). If month is absent in the minimum model, a single curve is shown. The floral density of trees was not relevant at site R or in January, thus they were removed from data analysis. Abbreviations for sites: FS (Foyel Sur), FN (Foyel Norte), R (Los Repollos).

conifer forest characterized by frequent fires and forest understory species-rich in pollen and nectar (Galbraith et al., 2019). This study showed that the effect of salvage logging after fire on flowering plant density was greater during the latter half of the season, with consequences for the habitat conditions of bees (Galbraith et al., 2019). In summary, previous studies have evaluated different aspects related to the availability of floral resources and the general pattern indicates that certain levels of biomass removal associated with forest management increase them.

HI had a positive effect on the density of most groups of floral visitors, which is related to an increase in native floral density. Other studies found that logging promoted the abundance of native bees (Romey et al., 2007), bumblebees (Pengelly and Cartar 2010), and butterflies (Korpela et al., 2015), associated with an increase in floral resources. It is difficult to compare other groups of floral visitors due to the lack of experimental studies; but in grasslands, the activity of beetles, bumblebees, and

muscoïd flies was positively related to blossom density (Hegland and Boeke 2006). Honey bees probably did not respond to thinning because their density is related to the floral density of native shrubs, whose response to harvesting is of a lesser magnitude than that of native herbs.

Such general positive responses of floral visitors were more related to the prevalence of generalist interactions than invader complexes; because native plant floral density, especially that of herbs, was enhanced by HI. *Bombus terrestris* (the most common bumblebee, Coulin et al., 2019), is considered a super-generalist species (Aizen et al., 2014). This explains why the density of exotic bumblebees had a positive trend in relation to the floral density of native herbs and not exotic herbs. Morales and Aizen (2002) also found that *B. ruderatus* visited exotic and native plants indistinctly. Halictids, the most common bee family in our sites, also visit many plant species (González-Vaquero and Roig-Alsina, 2019), while hoverflies also had a consistently positive response to HI and are typically considered as generalists (Lucas et al., 2018). In sum,

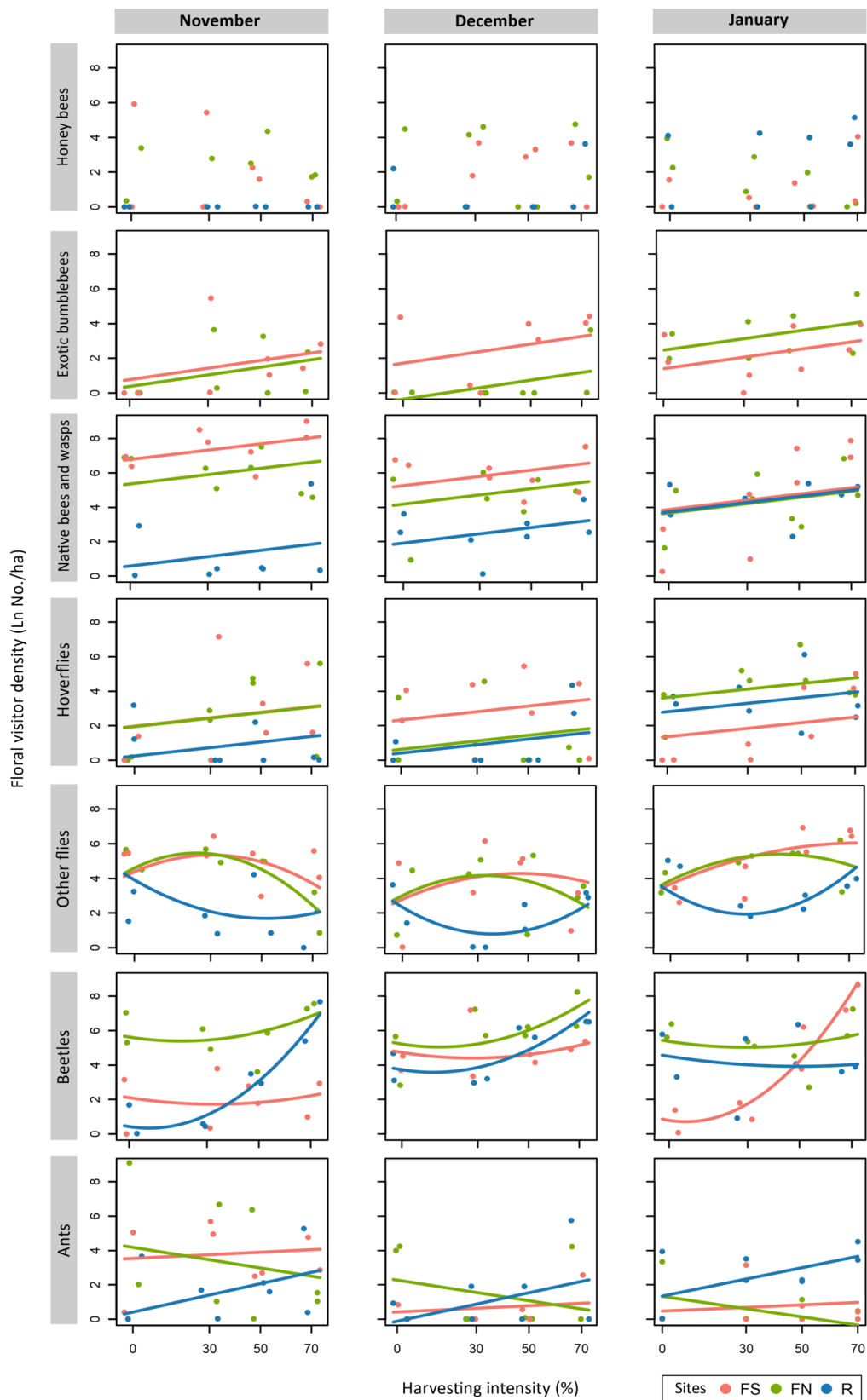


Fig. 2. Effect of harvesting intensity (HI) on the density of honey bees, exotic bumblebees and native bees and wasps, hoverflies, other flies, beetles and ants for the main flowering months and for each site. Dots correspond to the average value of a plot, and curves represent the predicted values from mixed-effect models. Curves are absent if HI is not included in the minimum adequate model selected by AIC (Akaike Information Criteria). The density of exotic bumblebees was not relevant at site R. Abbreviations for sites: FS (Foyel Sur), FN (Foyel Norte), R (Los Repollos).

Table 3

Spearman correlation coefficients between the floral density (Ln No./ha) of plant groups (exotic herbs, native herbs, native shrubs and native trees) and floral visitor density (Ln No./ha) groups (honey bees, exotic bumblebees, native bees and wasps, hoverflies, other flies, beetles and ants). Significance codes: **, $P \leq 0.05$; *, $P = 0.05-0.1$.

Plant groups	Floral visitors						
	Honey bees	Exotic bumblebees	Native bees and wasps	Hoverflies	Other flies	Beetles	Ants
Exotic herbs	-0.10	-0.01	-0.05	0.12	-0.14	-0.25**	0.11
Native herbs	0.17	0.26*	0.12	0.30**	0.07	0.41**	-0.22*
Native shrubs	0.32**	-0.18	0.58**	0.24**	0.38**	0.02	0.41**
Native trees	0.09	-0.07	0.54**	0.10	0.14	-0.26	0.39**

these three groups are well-represented by generalist species capable of taking advantage of the increase in floral resources.

For the other groups of floral visitors, other variables besides flower density appear to modulate the HI effect. For beetles and ants of northern Patagonia, the type of habitat, as well as the taxonomic group in question, determines the response to another type of local disturbance: fire (Farji-Brener et al., 2002, Sackmann and Farji-Brener, 2006). In particular, woody vegetation cover is a relevant variable that can affect the abundance of both groups (Farji-Brener et al., 2002, Baudino et al., 2020). These may explain the interaction between HI and site, while a replacement of species may explain the interaction with month for beetles. Furthermore, the woody cover probably modulates the floral density of herbs which was negatively correlated with the density of ants (native herbs) and beetles (exotic herbs), making their responses more complex. It is not possible to assume what factors modulate the effect on flies because very little is known about the ecology of these insects in the studied region.

5. Conclusions

Contrary to what the invader complex hypothesis states, our results show that the increase in exotic bumblebees density to harvesting is not explained by the changes in exotic floral density. Instead, the response of this group, like that of native bees and wasps group and hoverflies coincides with the increase in the density of native flowers, as predicted by the prevalence of generalist interactions. These group responses are independent of woodland contrasting conditions and the period of the flowering season. However, the response of flies, beetles, and ants to harvest was complex because these floral visitors seem to be driven simultaneously by other factors besides flower density. Because HI had a positive effect on the density of exotic bumblebees and exotic flowers in some sites, it can favor invasion if it also involves increased reproductive

performance

It is necessary to determine the prevalence in the long term of the observed patterns to understand the consequences at the community level. At the studied woodland sites, the resprouting capacity of the dominant plant species could lead to rapid closure of the canopy and reduce changes in plant-pollinators assemblages (Goldenberg et al., 2020, Matula et al., 2020). Indeed, the resilience associated to plant functional diversity of this type of communities is positively associated with site productivity (Chillo et al., 2020). Future studies should address pattern prevalence at contrasting woodlands but also incorporate the effect of disturbance frequency, which would represent a more realistic management scenario. Special attention should be paid to those groups with complex responses with an emphasis on discovering modulating factors.

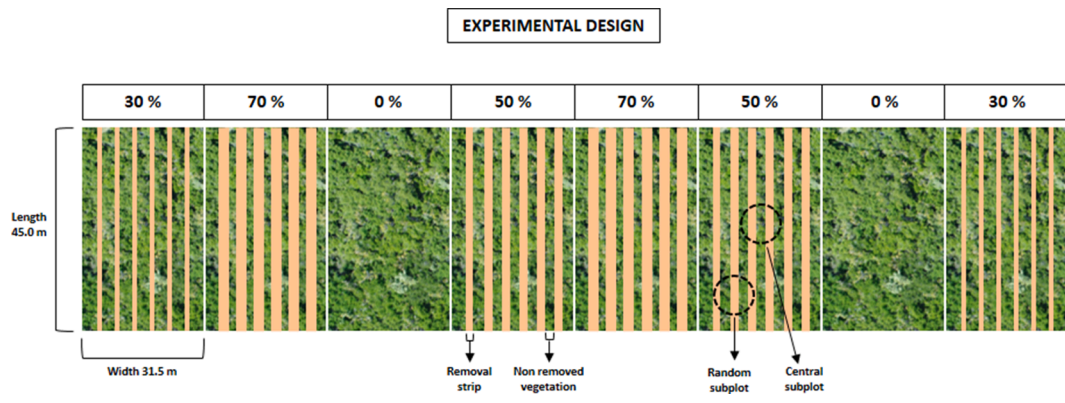
Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Lucas Alejandro Garibaldi reports financial support was provided by AGENCIA NACIONAL DE PROMOCIÓN DE LA INVESTIGACIÓN, EL DESARROLLO TECNOLÓGICO Y LA INNOVACIÓN.

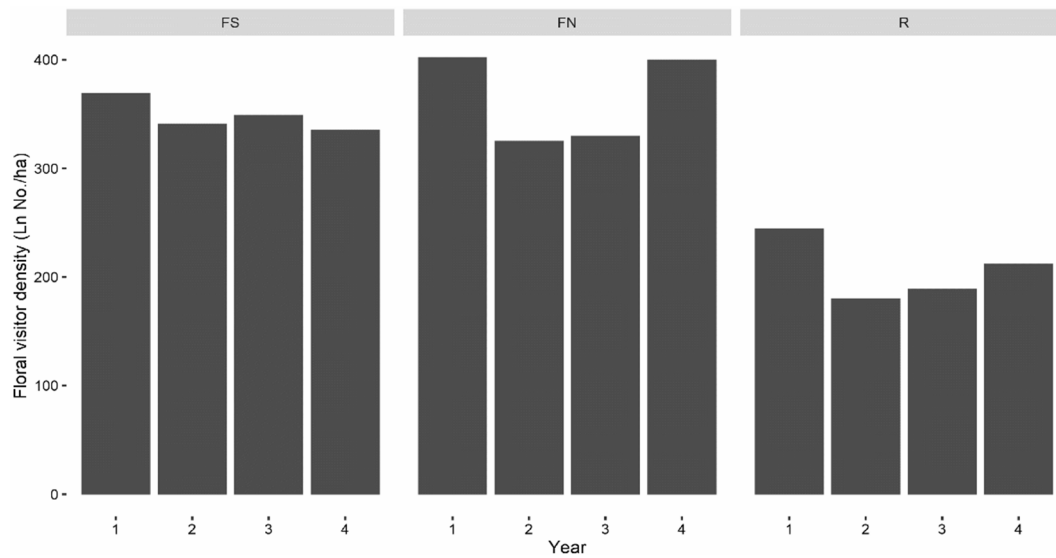
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Appendix 1. Experimental design for a site showing plots with their measurements and treatments. The percentage corresponds to the removed amount of woody plant cover according to each treatment. The removal strips whose width varies according to the treatment, the remaining vegetation and the two circular subplots (radius of 4 m) to measure the density of flowers are also shown.



Appendix 2. Total floral visitor density for each site and year of observation. Abbreviations: FS (Foyel Sur), FN (Foyel Norte), R (Los Repollos).



Appendix 3. List of plant species with biotic pollination present at the three sites, including scientific name, family, growth habit (herb, shrub or tree) and status (exotic or native).

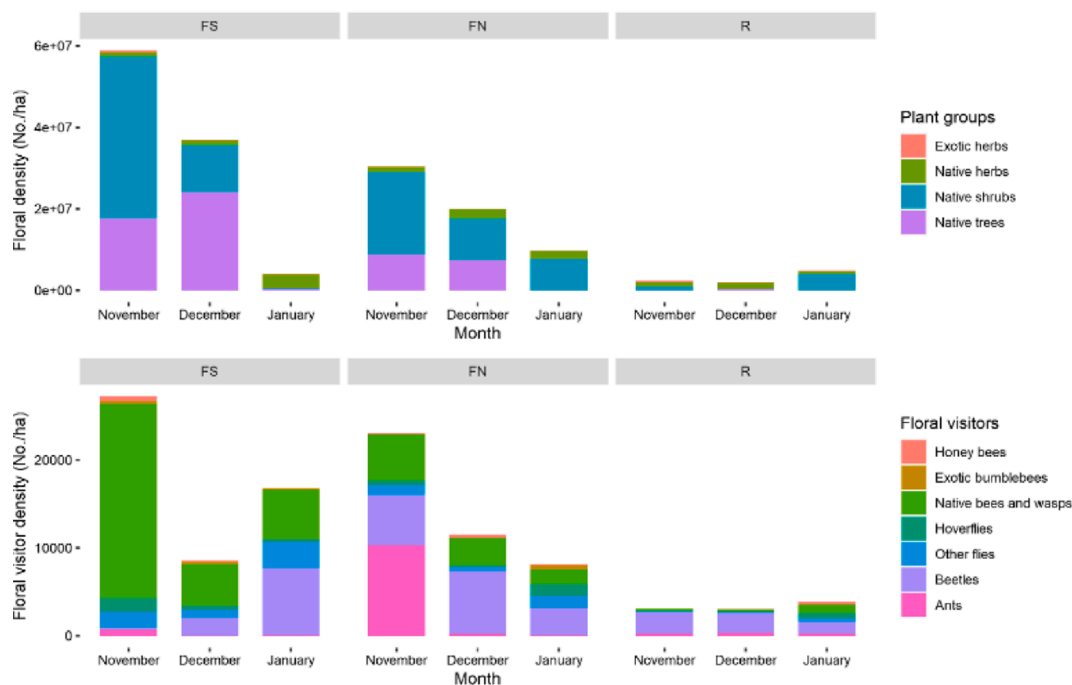
Plant species	Family	Habit	Status
<i>Cardamine hirsuta</i> L.	Brassicaceae	Herb	Exotic
<i>Carduus thoermeri</i> Weinm.	Asteraceae	Herb	Exotic
<i>Cerastium arvense</i> L.	Caryophyllaceae	Herb	Exotic
<i>Cirsium vulgare</i> (Savi) Ten.	Asteraceae	Herb	Exotic
<i>Claytonia perfoliata</i> Donn ex Willd.	Montiaceae	Herb	Exotic
<i>Conium maculatum</i> L.	Apiaceae	Herb	Exotic
<i>Crepis capillaris</i> (L.) Wallr.	Asteraceae	Herb	Exotic
<i>Draba verna</i> L.	Brassicaceae	Herb	Exotic
<i>Hypericum perforatum</i> L.	Hypericaceae	Herb	Exotic
<i>Medicago</i> sp.	Fabaceae	Herb	Exotic
<i>Prunella vulgaris</i> L.	Lamiaceae	Herb	Exotic
<i>Taraxacum</i> sp.	Asteraceae	Herb	Exotic
<i>Trifolium repens</i> L.	Fabaceae	Herb	Exotic
<i>Veronica serpyllifolia</i> L.	Plantaginaceae	Herb	Exotic
<i>Acaena ovalifolia</i> Ruiz & Pav.	Rosaceae	Herb	Native
<i>Acaena pinnatifida</i> Ruiz & Pav.	Rosaceae	Herb	Native
<i>Acaena</i> sp.	Rosaceae	Herb	Native
<i>Adesmia cf. parvifolia</i> Phil.	Fabaceae	Herb	Native
<i>Alstroemeria aurea</i> Graham	Alstroemeriaceae	Herb	Native
<i>Anemone multifida</i> Poir.	Ranunculaceae	Herb	Native
<i>Arjona</i> sp.	Schoepfiaceae	Herb	Native
<i>Chloraea alpina</i> Poepp.	Orchidaceae	Herb	Native
<i>Chloraea magellanica</i> Hook. f.	Orchidaceae	Herb	Native
<i>Chloraea</i> sp.	Orchidaceae	Herb	Native
<i>Codonorchis lessonii</i> (Brongn.) Lindl.	Orchidaceae	Herb	Native
<i>Collomia biflora</i> (Ruiz & Pav.) Brand	Polemoniaceae	Herb	Native
<i>Eryngium paniculatum</i> Cav. & Dombey ex F. Delaroché	Apiaceae	Herb	Native
<i>Euphorbia collina</i> Phil.	Euphorbiaceae	Herb	Native
<i>Galium hypocarpium</i> (L.) Endl.	Rubiaceae	Herb	Native
<i>Gamocarpha selliana</i> Reiche	Calyceraceae	Herb	Native
<i>Gavilea</i> sp.	Orchidaceae	Herb	Native
<i>Geranium magellanicum</i> Hook. f.	Geraniaceae	Herb	Native
<i>Geum</i> sp.	Rosaceae	Herb	Native
<i>Grindelia chilensis</i> (Cornel.) Cabrera	Asteraceae	Herb	Native
<i>Haplopappus</i> spp.	Asteraceae	Herb	Native
<i>Lathyrus</i> sp.	Fabaceae	Herb	Native
<i>Madia sativa</i> Molina	Asteraceae	Herb	Native
<i>Osmorhiza berteroi</i> DC.	Apiaceae	Herb	Native

(continued on next page)

(continued)

Plant species	Family	Habit	Status
<i>Oxalis valdiviensis</i> Barnéoud	Oxalidaceae	Herb	Native
<i>Phacelia secunda</i> J.F. Gmel.	Boraginaceae	Herb	Native
<i>Pinnasa bergii</i> (Hieron.) Weigend & R.H. Acuña	Loasaceae	Herb	Native
<i>Polygala cf. salasiana</i> Gay	Polygalaceae	Herb	Native
<i>Pseudognaphalium</i> sp.	Asteraceae	Herb	Native
<i>Quinchamalium chilense</i> Molina	Schoepfiaceae	Herb	Native
<i>Sisyrinchium arenarium</i> Poepp.	Iridaceae	Herb	Native
<i>Sisyrinchium chilense</i> Hook.	Iridaceae	Herb	Native
<i>Solidago chilensis</i> Meyen	Asteraceae	Herb	Native
<i>Stellaria</i> sp.	Caryophyllaceae	Herb	Native
<i>Tristagma patagonicum</i> (Baker) Traub	Amaryllidaceae	Herb	Native
<i>Vicia nigricans</i> Hook. & Arn.	Fabaceae	Herb	Native
<i>Vicia cf. magellanica</i> Hook. f.	Fabaceae	Herb	Native
<i>Viola reichei</i> Skottsbl.	Violaceae	Herb	Native
<i>Potentilla chiloensis</i> (L.) Mabb.	Rosaceae	Herb	Native
<i>Azorella prolifera</i> (Cav.) G.M. Plunkett & A.N. Nicolas	Apiaceae	Shrub	Native
<i>Baccharis magellanica</i> (Lam.) Pers.	Asteraceae	Shrub	Native
<i>Baccharis obovata</i> Hook. & Arn.	Asteraceae	Shrub	Native
<i>Berberis darwinii</i> Hook.	Berberidaceae	Shrub	Native
<i>Berberis microphylla</i> G. Forst.	Berberidaceae	Shrub	Native
<i>Calceolaria</i> spp.	Calceolariaceae	Shrub	Native
<i>Chiliotrichum diffusum</i> (G. Forst.) Kuntze	Asteraceae	Shrub	Native
<i>Diostea juncea</i> (Gillies & Hook. ex Hook.) Miers	Verbenaceae	Shrub	Native
<i>Escallonia virgata</i> (Ruiz & Pav.) Pers.	Escalloniaceae	Shrub	Native
<i>Fabiana imbricata</i> Ruiz & Pav.	Solanaceae	Shrub	Native
<i>Gaultheria mucronata</i> (L. f.) Hook. & Arn.	Ericaceae	Shrub	Native
<i>Maytenus chubutensis</i> (Speg.) Lourteig, O'Donell & Sleumer	Celastraceae	Shrub	Native
<i>Maytenus</i> sp.	Celastraceae	Shrub	Native
<i>Mutisia decurrens</i> Cav.	Asteraceae	Shrub	Native
<i>Mutisia spinosa</i> Ruiz & Pav.	Asteraceae	Shrub	Native
<i>Ribes cucullatum</i> Hook. & Arn.	Grossulariaceae	Shrub	Native
<i>Ribes magellanicum</i> Poir.	Grossulariaceae	Shrub	Native
<i>Schinus patagonicus</i> (Phil.) I.M. Johnst. ex Cabrera var. <i>patagonicus</i>	Anacardiaceae	Shrub	Native
<i>Aristolelia chilensis</i> (Molina) Stuntz	Elaeocarpaceae	Tree	Native
<i>Discaria chacaye</i> (G. Don) Tortosa	Rhamnaceae	Tree	Native
<i>Embothrium coccineum</i> J.R. Forst. & G. Forst.	Proteaceae	Tree	Native
<i>Lomatia hirsuta</i> (Lam.) Diels	Proteaceae	Tree	Native

Appendix 4. Floral density according to each plant group for the main flowering months and for each of the studied sites (first panel). Floral visitor density according to groups for the main flowering months and each of the studied sites (second panel). Abbreviations for sites: FS (Foyel Sur), FN (Foyel Norte), R (Los Repollos).



Appendix 5. Influence of M (month), S (site), HI (harvesting intensity) and HI² (squared harvesting intensity) on floral density of plant groups (exotic herbs, native herbs, native shrubs and native trees); and on floral visitor density (honey bees, exotic bumblebees, native bees and wasps, hoverflies, other flies, beetles and ants). The relative importance of each variable based on Akaike model weights is shown. Values of relative importance lower than 0.20 were removed from the table for clarity.

Variable	Plant groups				Floral visitors						
	Exotic herbs	Native herbs	Native shrubs	Native trees	Honey bees	Exotic bumblebees	Native bees and wasps	Hoverflies	Other flies	Beetles	Ants
M	0.81	1.00	1.00	0.31	0.20	0.90	1.00	0.90	1.00	1.00	1.00
S	1.00	0.36	1.00	0.44	0.40	0.75	1.00	0.60	1.00	1.00	0.88
HI	0.72	0.95	0.49	0.31	0.25	0.45	0.48	0.56	0.59	0.25	0.60
HI ²	0.77	0.43	0.51	0.27	0.25	0.61	0.76	0.40	0.71	1.00	0.41
M:S		0.23	1.00			0.61	1.00	0.42		0.99	0.85
M:HI		0.20					0.20		0.23		
M:HI ²							0.25		0.50	0.97	
S:HI	0.52								0.34		0.50
S:HI ²	0.66								0.35	0.97	0.25
M:S:HI											
M:S:HI ²										0.97	

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