



## Designing crop pollination services: A spatially explicit agent-based model for real agricultural landscapes

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### ABSTRACT

The decline of pollinators is a widespread problem in today's agriculture, affecting the yield of many crops. Improved pollination management is therefore essential, and honey bee colonies are often used to improve pollination levels. In this work, we applied a spatially explicit agent-based model for the simulation of crop pollination by honey bees under different management scenarios and landscape configurations. The model includes 1) a representation of honey bee social dynamics; 2) an explicit representation of resource dynamics; 3) a probabilistic approach to the foraging site search process; and 4) a mechanism of competition for limited resources. We selected 60 sample units from the rural landscape of the Chilean region with the largest apple-growing area and evaluated the effectiveness of different pollination strategies in terms of number of visits and number of pollinated flowers per hectare of apple crops. Finally, we analyzed how the effects of these practices depended on the structure of adjacent landscapes. Higher colony density per hectare in the focal crop increased the number of honey bee visits to apple inflorescences; however, the effects were nonlinear for rates of pollinated flowers, suggesting that there is an optimum beyond which a greater number of honey bees does not signify increased levels of crop pollination. Furthermore, high relative proportions of mass flowering crops and natural habitats in the landscape led to a decrease in honey bee densities in apple fields in landscapes with high relative cover of apple orchards (dilution effect). Our results indicate that for optimal crop pollination, strategies for management of pollinator species should consider the modulating effects of the surrounding landscape on pollination effectiveness. This model could thus be a useful tool to help farmers, beekeepers, and policy-makers plan the provision of pollination services, while also promoting the biodiversity and sustainability of agroecosystems.

### 1. Introduction

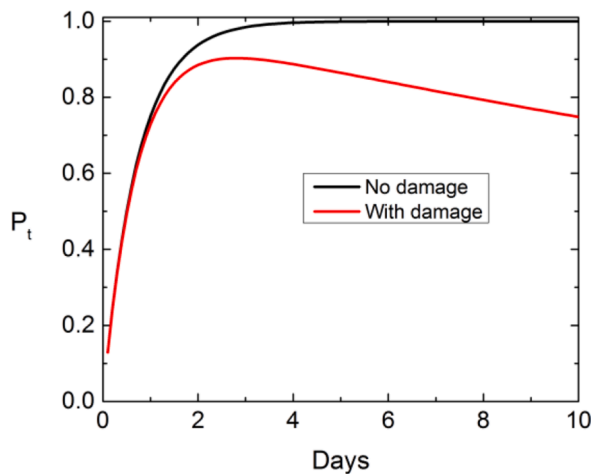
There is widespread recognition that the absence or shortage of pollinators is limiting crop yields around the world (Garibaldi et al., 2011), and managed honey bee colonies are commonly used to address this problem. The European honey bee (*Apis mellifera*) is the most widely managed species, both in open pollination (fields) and enclosed systems (Garibaldi et al., 2017). Managed honey bee colonies have certain advantages: they can be supplied on demand to coincide with blooming, and the location of colonies in the crop is relatively unconstrained

(Cunningham et al., 2016). However, even though biotic pollination is important for many crops (Potts et al., 2016), it is rarely monitored (Garibaldi et al., 2020).

Current management strategies for optimal pollination commonly involve providing managed pollinators, such as honey bees, at times of high demand. Indeed, many pollination reference handbooks (e.g., Delaplane and Meyer, 2000; Lesser Preuss, 2004) and empirical evidence (Isaacs and Kirk, 2010; Howlett et al., 2015; Cunningham et al., 2016) suggest placing a particular number of honey bee colonies per crop-cultivated area, to saturate crop flowers with foraging bees brought

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**Fig. 1.** Fraction of pollinated flowers as a function of time, showing the effect of damage by over-visiting. This value of  $\lambda$  is used throughout the study.

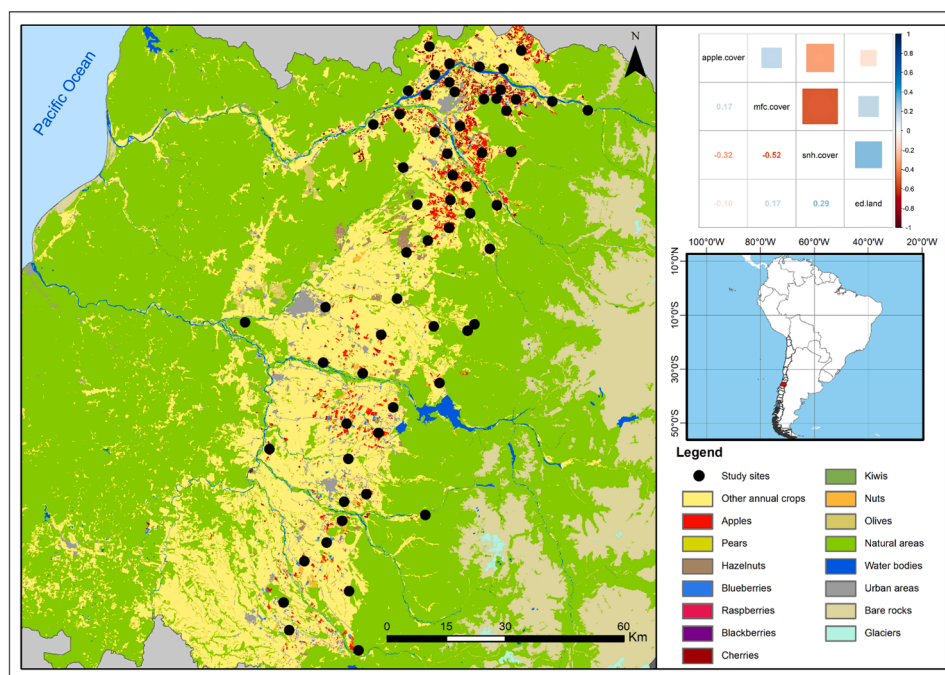
in at the beginning of the target crop blooming period (James and Pitts-Singer, 2008). Colony density is only one aspect of the strategy; optimal pollination also depends on the spatial organization of honey bee colonies, since distance between colony placements may influence the spatial pattern of bee activity, affecting the depletion rate of pollen from flowers (Cunningham et al., 2016). Except in some highly pollinator-dependent crops (e.g., almonds) where the use of managed pollinators is routine, the effectiveness of managed pollination practices has been under-studied.

Understanding how landscape structure (i.e., landscape composition and configuration) determines the densities of functionally relevant species is critical for maintaining ecosystem services, like pollination, in anthropogenically transformed landscapes (Tschamkete et al. 2012). Movement across habitats is a common phenomenon in many species, and the spillover of pollinators from natural habitats to agroecosystems has been well documented in human-dominated landscapes (Garibaldi

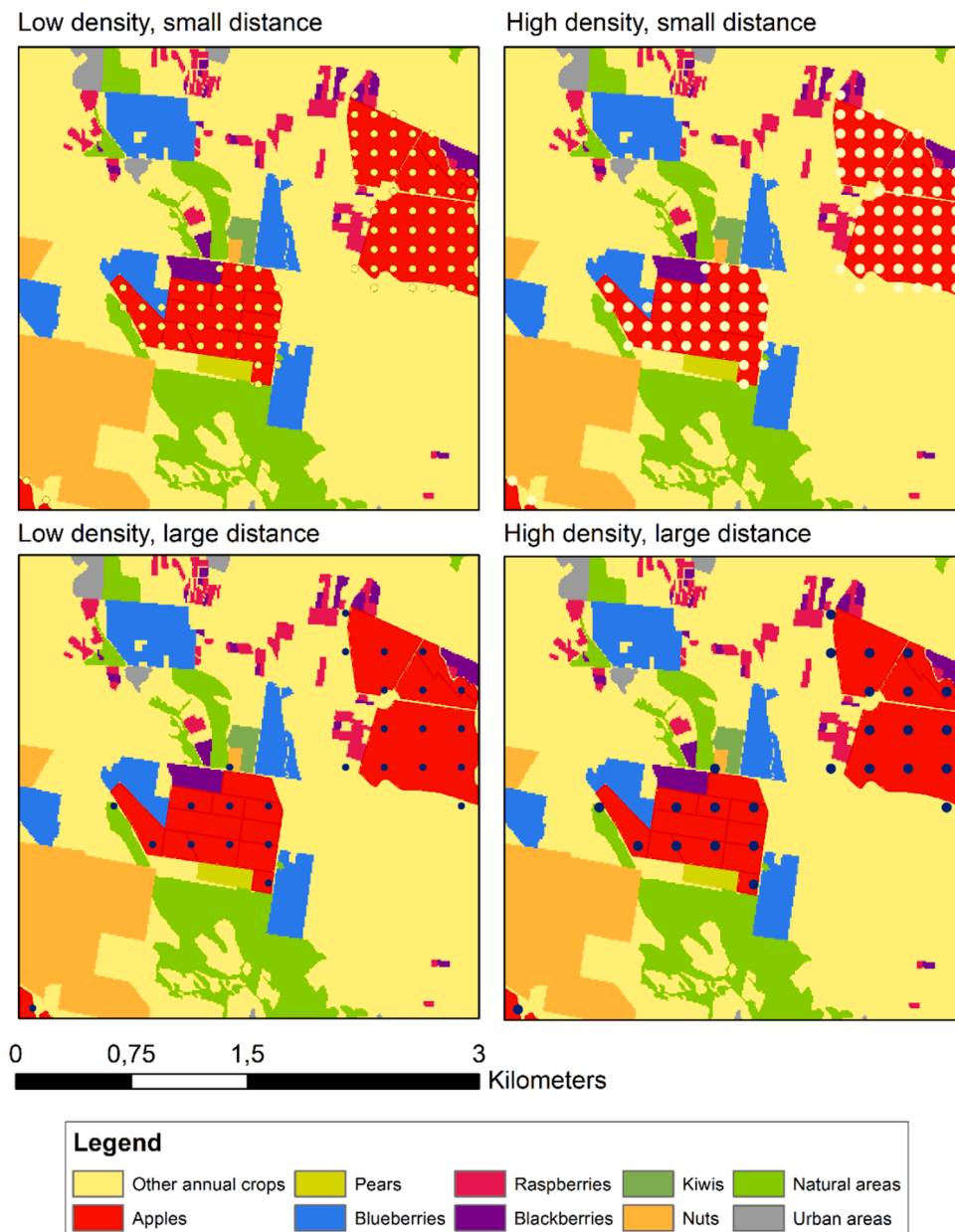
et al., 2011). While there is much evidence for spillover from natural habitats to managed areas, little attention has been given to flow in the opposite direction (Blitzer et al., 2012). For instance, mass-flowering crops may alter pollination services to other simultaneously blooming crops, either decreasing pollination via competition for pollinators or facilitating it via pollination spillover (Holzschuh et al., 2011; Holzschuh et al., 2016; Osterman et al., 2021). The response of managed honey bee abundance and service to landscape predictors is nonlinear, and depends on interactions between landscape composition and configuration, and the pollination strategy used. Nevertheless, to our knowledge this has not been examined.

Mechanistic models can help us investigate the implications of colony management practices for crop pollination, and their interaction with landscape structure effects. Many models have been developed to explore how pollination services are delivered across landscapes, and how these services are affected by changes in landscape structure. Several of these models include a spatial dimension and incorporate seasonal aspects of floral resources and population dynamics (Lonsdorf et al., 2009; Zulian et al., 2013; Olsson and Bolin, 2014; Olsson et al., 2015; Häussler et al. 2017). Some spatially explicit models can also predict how management interventions in a particular landscape affect pollination (Olsson et al., 2015; Häussler et al. 2017) and address the impact of various combinations of stressors on pollinators (Becher et al., 2018; Becher et al., 2016; Becher et al., 2014). Although these models are of interest in addressing this question, they assume that there is no resource depletion, which is key to understanding honey bee foraging behavior, and particularly how exploitative competition can affect foraging site choice (Inouye 1978; Balfour et al., 2015). One exception is the paper by Bolin et al. (2018) that demonstrates the existence of a coexistence mechanism by developing a spatially explicit mechanistic model for exploitative competition, using an existing general framework for habitat selection by central place foragers (Olsson et al., 2008, 2015; Olsson and Bolin 2014). However, this model has no relation to the use of managed honey bee colonies for crop pollination.

Furthermore, although some models can provide relative measures of pollinator visitation to crops (Lonsdorf et al., 2009; Zulian et al., 2013) or relatively realistic predictions of visitation rates (Becher et al.,



**Fig. 2.** Land cover map of the Maule region in Chile and location of landscape sample units. The units are square areas of 900 ha, selected to encompass a gradient of proportional area occupied by apple crops within the landscape sampling units. Upper right corner: Spearman correlations between landscape variables. The central inset shows the location of the Maule region in Chile, South America.



**Fig. 3.** Graphical display of the generation of treatments in the factorial experiment that combined colony density per hectare under apple cultivation (with two levels) and distance between groups of colonies within apple crops (with two levels).

2014; Olsson et al., 2015; Häussler et al. 2017), they do not incorporate process-based ecological production functions that would enable assessment of the effects of pollination levels on crop fruit set. One exception is the spatially explicit simulation model developed by Sáez et al. (2018b), which addresses the processes of pollen removal and deposition within apple orchards, with emphasis on how the spatial design of trees in orchards and honey bee locations modify the pollination process. However, the spatial scale considered (a field of 1 ha) does not allow examination of how landscape structure moderates pollinator performance on pollinator-dependent crops.

In this study, we assess the effect of honey bee colony management on apple pollination in the central-southern region of Chile, considering particularly the number of colonies per hectare and their spatial arrangement. We also analyze how the effects of these strategies differ according to the characteristics of the surrounding landscape. To this end, we apply a spatially explicit agent-based model (Joseph et al.,

2020) to simulate the pollinator activity of honey bees in real agricultural landscapes; we expand the model by incorporating an ecological production function that describes the pollination and post-pollination processes that determine fruit set.

## 2. Materials and methods

### 2.1. Honey bee colonies

We used a spatially explicit agent-based model (Joseph et al., 2020) to simulate crop pollination by honey bees. This model represents honey bee colonies as unique and independent entities that interact with each other through their local environment. Another important characteristic of the colonies is that they have adaptive behavior, i.e., they collect nectar and pollen from food sources in the surrounding landscape to store in their nest and feed to the brood. However, to exploit a food

**Table 1**

Estimated parameters and 95% confidence intervals (CIs) for each predictor variable in the best-ranked models relating the number of visits and the number of pollinated flowers in apple crops. Only significant main effects and interactions are shown (Appendix C).

	No. visits • ha <sup>-1</sup> • day <sup>-1</sup>		No. pollinated flowers • ha <sup>-1</sup> • day <sup>-1</sup>	
	Predictor	Estimate (CI 95%)	Predictor	Estimate (CI 95%)
intercept	4.221.829	(3.671.148, 4.772.509,5)	599.267	(549.297, 649.237)
Density (cph)	1.573.820	(1.040.449,3, 2.107.190,9)	304.531	(247.589, 361.473)
ln (apple cover)	1.751.169	(1.594.855,1, 1.907.482,9)	350.022	(311.899, 388.144)
ln (apple cover) <sup>2</sup>	–	–	-28.927	(-38.073, -19.782)
mfc cover (%)	-87.130	(-104.070,9, -70.189,3)	-7.312	(-8.688, -5.936)
snh cover (%)	-53.630	(-60.534,8, -46.724,4)	-3.502	(-4.067, -2.939)
ed land (m • ha)	-2.962	(-6.196,8, 272,68)	-393	(-657, -129)
ln (apple cover): density	1.859.655	(1.643.792,8, 2.075.518,8)	109.859	(56.152, 163.565)
ln (Apple cover) <sup>2</sup> : density	–	–	-34.859	(-47.643, -22.075)

source, the bees need to find it in the first place. Because floral resources are limited, the food collected by a colony in a foraging site necessarily reduces the food available to other colonies at the site, affecting the foraging decisions and patch visitation rates of the bees and, in consequence, colony development and survival.

Each honey bee colony in the model is characterized by its location, its number of bees and its quantity of honey. Intra-colony demography and life history characteristics are based on the model proposed by Khoury et al. (2013), where colony growth is determined by food availability and its interaction with behavioral and social processes in the colony. The only difference is that while in this model the food stores increase proportionally to the number of foragers, in our model it increases with the daily gain of the foragers,  $G_t$ , which depends on the resource availability in the surrounding landscape. The equation for the amount of food that is stored in the hive and available for colony use is:

$$F_{(t+1)} = F_t - \gamma_A(n_f + n_w) - \gamma_B n_b + G_t, \tag{1}$$

with  $F_t$  representing the amount of food on day  $t$ ,  $\gamma_A$  the consumption of stored food by workers and foragers,  $\gamma_B$  the consumption of stored food by broods, and  $n_f$ ,  $n_w$ ,  $n_b$  are the number of foragers, workers and broods, respectively.

The Khoury et al. (2013) model uses simple differential equations to represent the transitions of eggs laid by the queen to brood, which then become hive bees and finally forager bees, and the process of social inhibition that regulates the rate at which hive bees begin to forage. The model assumes that food availability can influence both the number of broods successfully reared to adulthood and the rate at which bees transition from hive duties to foraging.

## 2.2. Land cover and floral resource dynamics

The input data for the model are from land cover maps, composed of a discrete number of land cover classes, where honey bee colonies can search for food. Each land cover class is paired to a resource carrying capacity ( $K$ ), a daily resource renewal rate ( $r$ ), a value for floral attractiveness for honey bees ( $FA$ ) and a flowering period. Carrying capacity ( $K$ ) is the amount of nectar and/or pollen resources available in each cell for a certain number of land-cover classes, which represent fields with crops or habitats with wild flowers. We assume that the carrying capacity is constant during the flowering period, and equal to zero the rest of the year, and that these resources are renewed daily at a constant rate  $r$  during the flowering period. We do not distinguish between pollen and nectar (protein and carbohydrates) here. Time evolves in discrete steps, with a time unit of one day. We keep the carrying capacity constant, assuming that the new flowers during the flowering period compensate for the loss of production due to pollination and damage (as implemented in Joseph et al. (2020)). Floral attractiveness was defined as a score ranging from zero (not at all attractive, never used) to one (very attractive, preferred over other flowers). We assume

that attractiveness scores reflect both attractiveness per se and nutritional quality. Scoring was based on literature and expert opinion (Koh et al., 2015; Zulian et al., 2013)(Appendix A).

The model uses land cover maps of 3 km by 3 km with a spatial resolution of 10 m, where bees can search for food sources. This precision level is small enough to capture the size of the *Apis mellifera* foraging area and large enough to be interesting in terms of their flight range, since not all colonies will be able to forage across the entire map. The maximum foraging distance has been set to 3 km so that bees can forage on almost all the map. It is known that bees can make trips farther than 3 km (Abou-Shaara, 2014), but these trips cannot be seen on the map as currently implemented. The average foraging distance of the bees is not a parameter of the model, but a result of the foraging process, and varies with the exponent  $\gamma$  of the preference function and with the distribution of the food sources in the landscape. The exponent  $\gamma$  represents the knowledge that the hive has of the resources in its surroundings.

The adoption of a foraging site by a group of foragers implies that they constantly come back to this site until the nectar source is exhausted (Lesser Preuss, 2004). In the model, each day a colony selects a number of foraging sites with a size of 30 m by 30 m (9 cells), where it will send a fraction of foragers to collect food. The number of foraging sites a colony visits each day is proportional to the number of foragers ( $n_f$ ) in the colony divided by the size of a squad ( $k$ ).

A honey bee colony selects their foraging sites at the beginning of each day, relying on information provided by scouting bees: the foraging resources at the sites and their distance from the colony. The probability of choosing a site  $(x, y)$  is defined as depending on  $R_t(x, y)$ , which is the total resource on a square lattice composed of a central cell  $(x, y)$  and the eight cells that surround it, and the flight cost of reaching them,  $f(d)$ :

$$P_{(x,y)} = \begin{cases} \frac{(R_t(x,y)f(d)^\gamma)}{\sum_{(u,v) \in r_f} (R_t(u,v)f(d)^\gamma)} & \text{if } d < r_f \\ 0 & \text{otherwise.} \end{cases} \tag{2}$$

where  $d$  is the Euclidean distance from the hive to  $(x, y)$  and  $r_f$  is the range of flight of the bees. The cost  $f(d)$ , normalized to the interval  $[0, 1]$ , is an affine decreasing function of  $d$ , with  $f(0) = 1$  and  $f(r_f) = 0$ . The exponent  $\gamma$  represents the knowledge that the colony have of the resource in its surroundings; if  $\gamma = 0$ , the colony chooses its foraging sites uniformly at random, and when  $\gamma \rightarrow \infty$ , the colony systematically chooses the site with the highest harvestable resource. The precise value of this parameter is less important than the general shape of the function, so there is some freedom to choose it within the boundaries of biological significance. We have used  $r_f = 3$  km and  $\gamma = 3$  as in Joseph et al., 2020.

Once the foraging sites have been selected, the colony sends a fraction  $v_i$  of foragers to each site  $i$ , also depending on resource availability



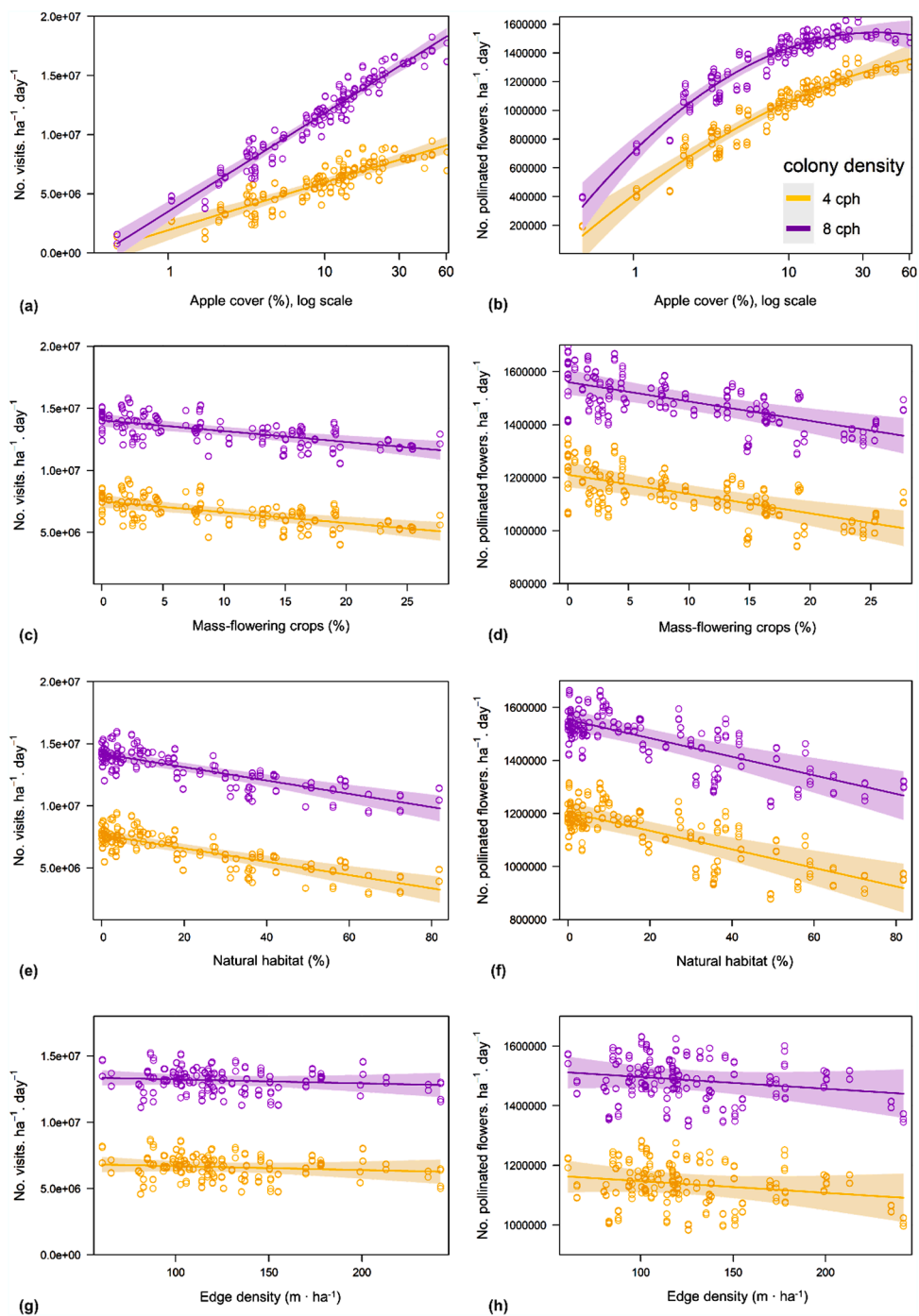
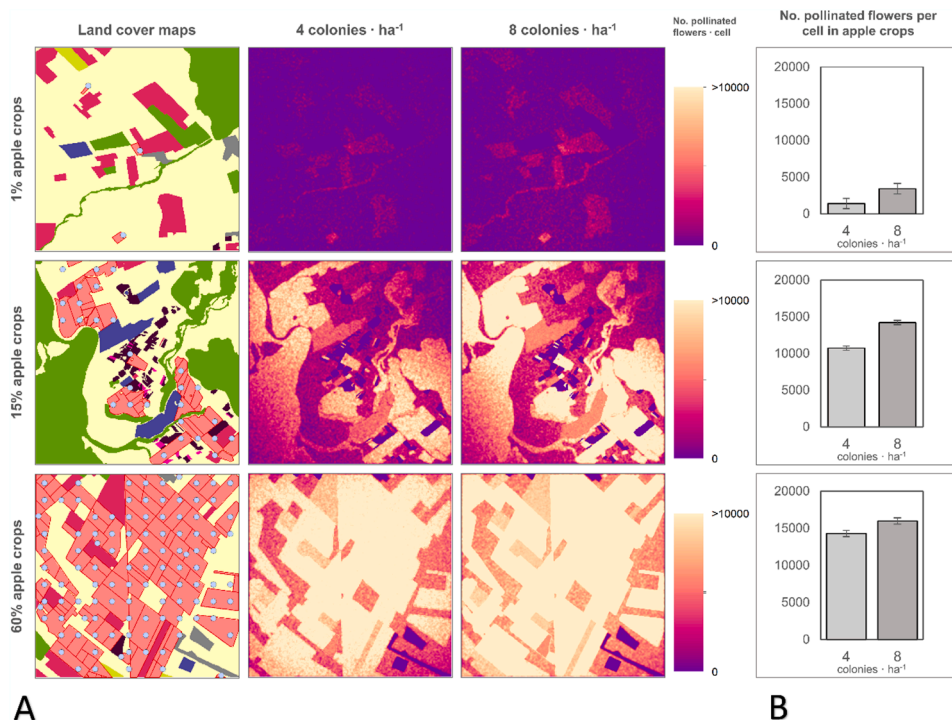


Fig. 4. Partial effects plots showing the effect of covariates on the number of visits (left column) and number of pollinated flowers (right column) in the apple crops. The fitted values are plotted on the y axis and the focal predictor on the x axis. These graphs give the partial effect of covariates, with all other predictors fixed at the mean.



**Fig. 5.** The output matrix of the average number of pollinated flowers per cell generated by the model. The upper row shows the landscape sampling unit with the minimum percentage of apple crops (0.47%), the middle row shows the landscape sampling unit with the average percentage of apple crops (14.47%), and the bottom row shows the landscape sampling unit with the maximum percentage of apple crops (60.6%). The plots on the right side of the figure show the average number of pollinated flowers per cell in apple crops for each colony density.

and distance from the hive ( $d$ ). This parameter ( $v_i$ ) is a weighting factor, so that the more foraging resources there are on a harvesting site, the more foragers are sent to it (Eq. (5), Joseph et al., 2020).

As a result of the foraging site selection process, several colonies may select the same foraging sites and compete for the resources (intra-specific competition). We implement this possibility of colony competition by sorting each day a random harvesting order  $\tau$  for each colony. Sorting this order at every time step averages the effect of the selected order. Through exploitation, colonies interact with each other indirectly, responding to a resource level that has been depressed by the activity of competitors ( $R_i^c(x, y)$ ). The probability of colonies choosing the same site is higher when the resource in their surroundings is globally low, and thus the competition is stronger.

Let  $R_i^c(x, y)$  correspond to the value of the resources after the turn of the colony which feeds at round  $\tau$ . The harvestable resources available for the next colony at the site is the product of  $R_i^c(x, y)$  and  $f(d)$ . Let  $c$  correspond to the maximum that a forager can carry back if the distance to the hive is null. If the resource is in excess, the foragers sent to the site collect the maximum quantity they can carry during the day,  $cf(d)v_k n_f$ , but if the resource is lower than this value, they take it all, and deplete the site. The daily gain of colony  $i$  at site  $(x, y)$  can then be described as follows:

$$g_{i,t}(x, y) = \min(cf(d)v_i n_f, R_i^c(x, y)) \quad (3)$$

The total daily gain of a colony is, then, the sum of all the local gains at its foraging sites,  $G_t = \sum_i g_{i,t}(x, y)$ .

### 2.3. Pollination function

In this work we expand the model of Joseph et al. (2020), incorporating an indicator of the level of crop pollination. This incorporation is directly related to scientific studies that estimate the number of visits required to fully fertilize the receptive ovules of a single flower (S.K.

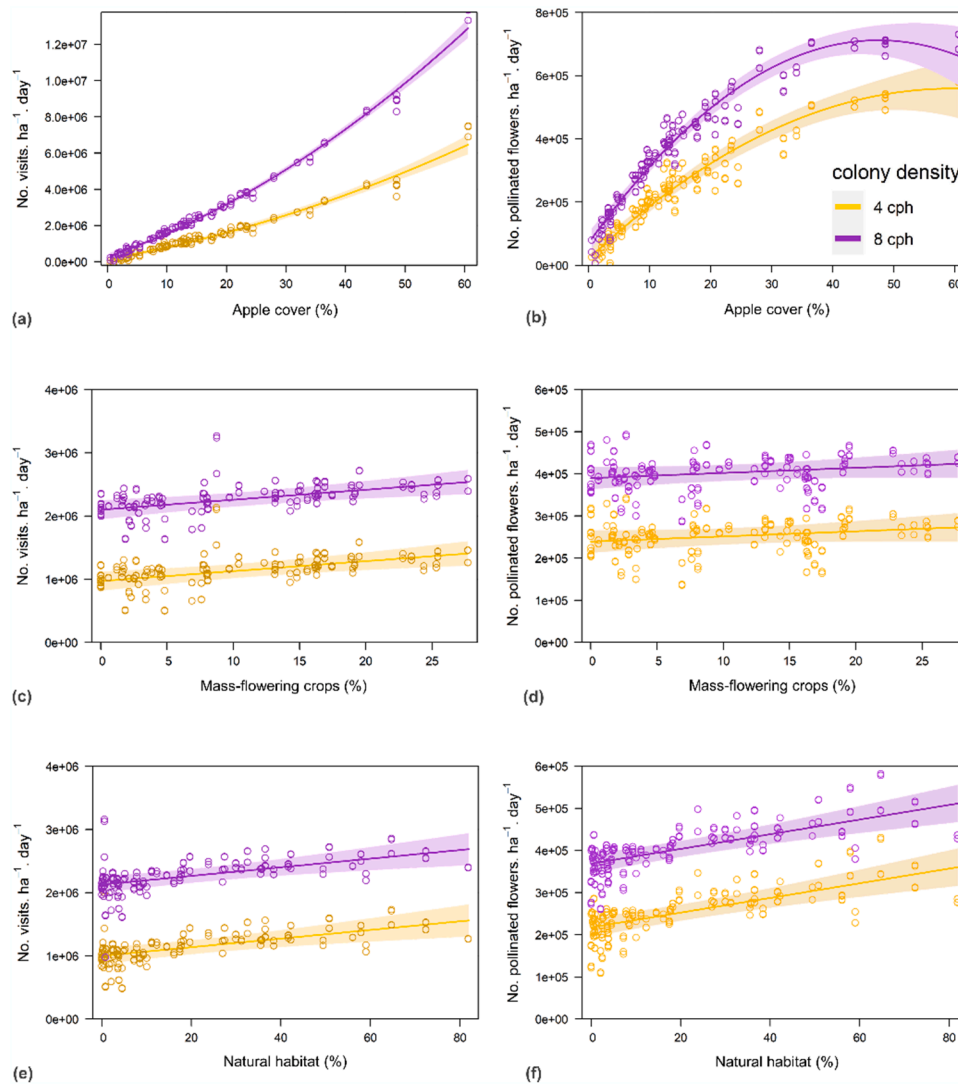
Vicens and Bosch 2000; S.K. Javoreck et al., 2002; Godwin et al., 2013; Sáez et al., 2014; Sáez et al., 2018a; Garibaldi et al., 2020). Let us formulate a model for the number of flowers successfully pollinated at each cell. This number depends on three factors: the number of flowers at the cell multiplied by the probability of pollination and by the probability of remaining viable. Both of these probabilities depend on the number of visits. If we call  $p$  the probability that a visit will lead to successful pollination (i.e., mean efficiency of one visit), the probability that a flower will be successfully pollinated after a number  $V_t$  of visits is  $1 - (1 - p)^{V_t}$ . Taking into account the damage that can be done to the flower (Cribb, 1990; Velthuis and Van Doorn, 2006; Morris et al., 2010; Badano and Vergara, 2011; Garibaldi et al., 2013; Sáez et al., 2014; Rollin and Garibaldi, 2019; Sáez et al., 2018a), let us say that each visit has a constant probability  $q$  of damage. After repeated visits the probability of remaining viable is  $(1 - q)^{V_t}$ , which can be recast as an exponential decaying with a constant rate (similar to that used in Sáez et al., 2018a). Thus, the proportion of flowers that will be pollinated can be written as:

$$P_t(x, y) = \exp(-\lambda V_t) (1 - (1 - p)^{V_t}) N_{\beta}(x, y) \quad (4)$$

where  $N_{\beta}(x, y)$  is the number of flowers in the cell,  $\lambda$  is a constant decay rate and  $V_t$  is the number of visits per flower per day. Fig. 1 shows the time dependence of this function.

The outputs of the model are two matrices: one represents the number of visits to each cell, while the second shows the number of pollinated flowers in each cell. Both variables have been used in other studies as a proxy for pollination efficiency (Rollin and Garibaldi, 2019). The output matrix of the simulation model using the equation of pollination and post-pollination processes is an innovation introduced into the model presented in Joseph et al. (2020).

We programmed the simulations in Spyder 3. All codes are written in Python using the CUDA module for GPU computation. All the parameters used for the colony model have been kept from the study by Khoury



**Fig. 6.** Partial effects plots showing the effect of covariates on the number of visits (left column) and number of pollinated flowers (right column) in the landscape surrounding the apple orchards. The fitted values are plotted on the y axis and the focal predictor on the x axis. These graphs give the partial effect of covariates, with all other predictors fixed at the mean.

**Table 2**

Estimated parameters and 95% confidence intervals (CIs) for each predictor variable in the best-ranked models relating the number of visits and the number of pollinated flowers in the surrounding landscape. Only significant main effects and interactions are shown (Appendix C).

Predictor	No. visits • ha <sup>-1</sup> • day <sup>-1</sup>		No. pollinated flowers • ha <sup>-1</sup> • day <sup>-1</sup>	
	Estimate	Estimate (CI 95%)	Estimate	Estimate (CI 95%)
intercept	-167.034	(-273.858, -60.209)	-24.794	(-43.555, -6.033)
density (cph)	168.791	(51.410, 286.172)	48.849	(29.234, 70.464)
apple cover)	58.537	(49.408, 67.667)	18.108	(16.505, 19.711)
apple cover) <sup>2</sup>	761	(588, 934)	-152	(-183, -122)
mfc cover (%)	15.798	(11.696, 19.901)	1.218	(498, 1939)
snh cover (%)	6.833	(5.244, 8.421)	1.742	(1.463, 2.021)
density: apple cover	54.856	(42.079, 67.634)	8.923	(6.679, 11.167)
density: apple cover <sup>2</sup> :	799	(556, 1.042)	-133	(-175, -90)

et al. (2013). A summary of the parameters and their values is provided in Appendix B.

**2.4. Baseline landscapes**

We focused on agricultural landscapes of the Maule region in Chile,

characterized by the heterogeneous distribution of grasslands and crop fields combined with plantation forestry and natural areas, mostly sclerophyllous forest. We used a national land cover map (Zhao et al., 2016) and the regional fruit census (ODEPA, 2016) to obtain a regional land cover map. First, we standardized the map classification to six land-use classes: croplands, natural and semi-natural habitats (hereafter,

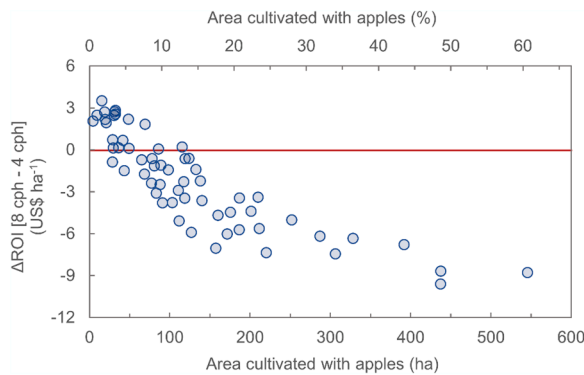


Fig. 7. Differences in the profitability of different management strategies (colonies per hectare, cph) as a function of the cultivated area within the landscape.

“natural habitats”), water bodies, urban areas, barren lands, and snow and ice. The natural habitats include forests, grasslands, shrubs and wetlands.

We then identified the fruit crops with the largest cultivated area in the region, based on the regional fruit census. The major crops were apples, cherries, olives, kiwis, walnuts, and pears, while hazelnuts, blueberries, raspberries and blackberries were cultivated on a smaller scale (ODEPA, 2016). Finally, we worked on the land cover classification scheme on a more detailed level, performing an overlay of the fruit crop classes in the cropland class, increasing the number of land cover classes to 16 in total (Appendix A). This map was resampled to change the cell size from 30 to 10 m, the spatial resolution at which the model works.

A total of 60 maps of 3 km x 3 km were selected along independent gradients of landscape composition (% of apple crops) and configuration (edge density) (Fig. 2;  $s_p = -0.10$ ,  $P = 0.43$ ). To determine landscape composition, on each map we quantified the percentage cover of apple crops, natural habitats, and mass-flowering crops. Mass-flowering crops included all fruit/nut crops present in the study landscapes whose flowering periods overlapped, at least in part, with apple crops (but did not include them). The flowering periods of cherries, pears, blueberries, raspberries and walnuts partially matched the apple blooming period (de la Cuadra et al. 2019).

We also calculated landscape configuration as the total length of edges per area of each map (edge density, in m/ha). Landscapes with high edge density increase opportunities for exchange, thus favoring the spillover of energy, resources and organisms across habitats, including between managed and natural ecosystems. This measure has been frequently used in other studies (Fahrig 2003; Martin et al., 2019; Nicholson et al., 2017). To obtain these landscape metrics we used Fragstats 4.2 software (McGarigal and Ene, 2014).

The percentage area covered by apple crops spanned a gradient of 0.5 to 60.6 percent (mean  $\pm$  SD  $14.5 \pm 12.9\%$ ), natural habitats covered a gradient of 0 to 81.8 percent (mean  $\pm$  SD  $19.3 \pm 21.2\%$ ) and mass-flowering crops spanned a gradient of 0 to 27.69 percent (mean  $\pm$  SD  $10.2 \pm 7.9$ ). Additionally, the selected maps covered a gradient of edge density within the range of 60.6 - 242.2 m/ha (mean  $\pm$  SD  $124.3 \pm 38.6$  m/ha).

## 2.5. Landscapes with simulated colony density and arrangement strategies

We generated management scenarios by adding honey bee colonies virtually, following a factorial design that combines two factors: colony density, with two levels (4 and 8 hives per ha of apple crop) and the distance between groups of colonies, also with two levels (125 and 250 m). A total of 4 total treatments and 60 replications were therefore carried out for each treatment.

We represented the distance between groups of colonies by treating

their location as the center of a circle whose diameter indicates the distance between groups. From this value we generated a network of circles for each distance on each map and estimated how many circles could fit inside each apple orchard. We considered the center of each circle as a colony group, so we used these coordinates to determine the spatial arrangement of colony groups within each apple orchard, for each treatment, on each map (Fig. 3).

To determine the number of colonies in each apple field for each selected colony density, we multiplied the number of colonies for each density level by the size of each focal crop field. We then divided the number of colonies in each apple field by the number of circles contained in each field, for each of the distance factor levels.

We considered only spring and summer seasons, when most crops bloom and the demand for honey bee colonies for crop pollination usually increases. Natural habitats begin to bloom in the spring and extend to summer due to their greater floral diversity; in contrast, crops have shorter blooming periods of around 30 days at different moments of both seasons, since not all crops bloom simultaneously. Most flowering, and therefore the demand for pollination services, occurs between August and November in the central-northern and central-southern regions of Chile (de la Cuadra et al. 2019; Estay, 2012).

Simulated honey bee colonies were active for 40 days. We considered a flowering period of 30 days for apple cultivars. Moreover, we included a period of 10 days, 5 days before and 5 after the beginning of flowering, which enabled us to incorporate the variability of times in pollination contracts; for instance, placement of the colonies.

## 2.6. Statistical analyses

We used general linear models with a normal error distribution to analyze the effects of landscape composition and configuration, crop pollination management, and the interaction between these variables, on the number of visits and the number of pollinated flowers per hectare in the apple fields. Visits to the apple crops were estimated as the average number of visits per hectare of apples cultivated, and visits to the adjacent landscape were estimated as the average number of visits per hectare of the landscape surrounding the apple crops. The numbers of pollinated flowers were estimated as the number of pollinated flowers by hectare of cultivated apple crops and the number of pollinated flowers per hectare of landscape adjacent to these crops. To avoid collinearity between variables, a non-parametric multiple correlation matrix expressed in a correlogram was performed using the Spearman correlation ( $s_p$ ) (Fig. 2). We checked for multicollinearity between our chosen variables using the variance inflation factor (VIF). Variance inflation factors (VIFs) for all predictors (colony density, apple cover, mass-flowering crops, natural habitats, edge density) were always lower than 1.8 in all models.

The models considered the effects of honey bee colony density (categorical variable), the distance between groups of colonies (categorical variable), the proportion of apple crops (quantitative variable), the proportion of mass-flowering crops (quantitative variable), the proportion of natural habitats (quantitative variable), the landscape edge density (quantitative variable) and their interactions. The squared focal crop proportion and the logarithm of the focal crop proportion were also included in order to consider nonlinear responses to the different colony management strategies.

We used multi-model inference (Burnham et al., 2011) to select the minimum adequate model by the lowest Akaike Information Criteria value (AIC), using the *model.sel* function of the *MuMin* package (Package ‘MuMin’) of the R version 4.1.1 statistical software (R Core Team, 2020). The objective of AIC model selection is to estimate the information loss when model  $g_i$  is used to approximate full reality ( $f$ ). A measure for the discrepancy between full reality and model  $g_i$  is given by the Kullback-Leibler (K-L) information quantity  $I(f, g_i)$ , which is equal to the negative Boltzmann’s (1877) generalized entropy.

Akaike (1973) has shown that choosing the model with the lowest



expected information loss is asymptotically equivalent to choosing a model  $M_i$ ,  $i = 1, 2, \dots, K$  that has the lowest AIC value. The AIC is defined as:

$$AIC_i = -2\log L_i + 2V_i, \quad (5)$$

where  $L_i$ , the maximum likelihood for the candidate model  $i$ , is determined by adjusting the  $V_i$  free parameters in such a way as to maximize the probability that the candidate model has generated the observed data. Eq. (5) shows that the AIC rewards descriptive accuracy via the maximum likelihood, and penalizes lack of parsimony according to the number of free parameters. The model with the smallest AIC value was selected as the 'best' among the models tested. The AIC differences  $\Delta_i = AIC_i - AIC_{min}$  were computed over all candidate models  $g_i$ . To quantify the plausibility of each model, given the data and the set of models, the 'Akaike weight'  $w_i$  of each model was calculated, where:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{j=1}^R \exp(-\frac{1}{2}\Delta_j)} \quad (6)$$

The 'Akaike weight' is considered as the weight of evidence in favor of model  $i$  being the actual best model of the available set of models (Burnham and Anderson, 2002; Burnham et al., 2011). We also estimated the relative importance ( $r_i$ ) of predictor variables  $x_j$  in the set of models with the *importance* function of the *MuMin* package (Package 'MuMin'), which sums the Akaike weights across all the models in the set where variable  $j$  occurs. Thus, the relative importance of variable  $j$  is reflected in the sum  $w + (j)$ . The larger the  $w + (j)$  the more important variable  $j$  is, relative to the other variables (Burnham and Anderson, 2002). Predictors with  $r_i > 0.6$  were considered strongly related to response variables.

We performed a graphical inspection of the models to evaluate their adequacy by plotting: i) standardized residuals against fitted values and the predictive variables and, ii) a quantile-quantile distribution of standardized residuals.

## 2.7. Return on investment analysis

Return On Investment (ROI) analysis was used to evaluate the efficiency of different colony management decisions in pollination. The definition of ROI used in finance is the ratio of net benefits to costs. The ROI calculation organizes a project's costs and benefits into a useful profitability measure.

We estimated the total number of fruits  $\bullet \text{ha}^{-1}$  by multiplying the number of pollinated flowers per hectare by the fruit-to-flower ratio of apple crops (0.1) (Hünicken et al., 2020). On average, 70% of apple production is sold (F. Torres, pers. com.). We obtained monthly wholesale values for apples at the closest reference markets from March to November 2019 (odepa.gob.cl/precios/avance-por-productos-de-frutas-y-hortalizas). The price depended on the quality of the fruit, which was estimated by its individual weight, so we selected an average size of 150 g (medium:  $130 < \text{weight} \leq 170$  g at  $0.70 \text{ US}\$ \bullet \text{kg}^{-1}$ ). Production costs (agrochemicals, salary, gasoline, etc., but rental of honey bee colonies excluded) averaged  $0.30 \text{ US}\$ \bullet \text{kg}^{-1}$ . The average price paid for colony rental for the whole pollination season was 42 US\$.

For each scenario, we estimated a farmer's profit in  $\text{US}\$ \bullet \text{ha}^{-1}$  as follows:

$$\text{Prof. apples} = (n_f * 0.1 * 0.7 * w * c * \text{sup}) - (n_f * 0.1 * 0.7 * w * 0.3 * \text{sup}), \quad (7)$$

where:

$n_f$  = number of pollinated flowers per hectare;

$w$  = mean weight of fruits harvested;

$c$  = price based on fruit weight;

$\text{sup}$  = area cultivated with apples (hectares);

We then calculated the ROI for all simulated management practices in pollination, as follows:

$$ROI = \frac{(\text{Prof. apples} - (\text{col} * p))}{(\text{col} * p)}, \quad (8)$$

Where  $\text{col}$  is the number of honey bee hives per crop-cultivated area, and  $p$  corresponds to rental price per colony. Finally, we calculated the difference in profitability between the different strategies to evaluate their efficiency ( $\Delta ROI$ )

$$\Delta ROI = (ROI_8 - ROI_4) \quad (9)$$

## 3. Results

### 3.1. Apple crops

The general linear models showed that for the number of visits and number of pollinated flowers the important predictors were colony density, proportions of focal crop, natural habitats, mass-flowering crops, and edge density in the landscape; distance between colony groups within the apple fields was not found to be important (see estimated coefficients of the models in Table 1, and the relative importance of each predictor variable in Appendix C).

Our results show that as apple cover increased, the number of visits per hectare to the crop increased; this increase was not constant, however, being more marked at low cover than at high cover of apple crops (Fig. 4a). The main difference in number of visits per hectare between treatments was that, on average, the number of visits increased more with a high density of honey bee colonies (8 per hectare) than with a low density (4 per hectare) for each 1% increase in the area of cultivated apples in the landscape (Appendix D).

With respect to the number of pollinated flowers per hectare, we observed that as apple cover increased within the landscape, the number of pollinated flowers also increased. However, the rate of increase was not constant, being more marked at low cover of apple crops than at high cover (Fig. 4b). This implies deceleration of the rate of increase in the number of pollinated flowers per hectare of the crop as crop cover in the landscapes increased (Fig. 5).

In apple crops, the number of flowers pollinated was explained by an interaction between the cover of apple crops and colony density (Table 1). In landscapes with a high cover of apple crops, the difference in the number of flowers pollinated between colony densities was lower than for low cover (Fig. 4b). In fact, when the cover of apple crops exceeded  $\approx 38\%$  of the landscape, the higher colony density generated a decrease in the number of flowers pollinated per hectare (Fig. 4b).

According to these models, the number of visits and the number of flowers pollinated decreased with each percentual increment in the cover of mass-flowering crops (Fig. 4c and Fig. 4d) and natural habitats (Fig. 4e and Fig. 4f) in the surrounding landscape, for both colony densities (Table 1). Finally, the number of visits and the number of flowers pollinated decreased with increasing edge density in the landscape. These relationships were consistent for both colony density factor levels (Fig. 4g and Fig. 4h).

### 3.2. Surrounding landscape

The general linear models showed that for both response variables the important predictors were colony density, and the proportions of

apple crops, natural habitats, and mass-flowering crops. The remaining predictors were not strongly related to the response variables (see estimated coefficients of the models in Table 1., and relative importance values in Appendix C).

In the landscapes surrounding the apple crops, the number of visits shows nonlinear increases with increasing cover of apple crops, both with 4 and 8 colonies per hectare (Fig. 6a; Table 2). Furthermore, as apple crop cover increased, the number of visits in the landscape increased more rapidly. However, the number of visits to the landscape varied with colony density. Comparing landscapes with the low and high colony densities, the model predicted a greater increase in the number of visits in landscapes with high colony density (Fig. 6a; Table 2).

In the case of the number of pollinated flowers in the landscape surrounding apple crops, the effect was different. The number of pollinated flowers in the surrounding landscape increased with increasing cover of apple crops, but this increase was not constant, being higher at low cover of apple crops and lower at high cover of apple crops (Fig. 6b; Table 2). This implies a decrease in the rate of increase of the number of pollinated flowers in the landscape. This decrease is even greater with higher honey bee colony density in apple crops. Thus, when the cover of apple crops in the landscape exceeded  $\approx 48\%$  of the total, the average rate of change became negative, indicating a decrease in the number of pollinated flowers in nearby patches within these landscapes. In the case of the lower colony density, this phenomenon was observed when the cover of apple crops in the landscape exceeded  $\approx 60\%$  of the total landscape (Fig. 6b; Table 2).

In the landscapes surrounding the apple crops, the number of visits and the number of pollinated flowers increased with increasing cover of mass-flowering crops, for both colony densities (Fig. 6c and Fig. 6d; Table 2). Finally, the number of visits and the number of pollinated flowers in the landscapes adjacent to the apple crops also increased with increasing cover of natural habitats, for both colony densities (Fig. 6e and Fig. 6f; Table 2).

### 3.3. Return on investment analysis

When analyzing the return on investment for the different colony management strategies, we observed that the average ROI for the scenarios where honey bee colonies were stocked at 8 per hectare was  $29.3 \pm 5.6$  US\$/ha (mean  $\pm$  SE), while for the scenarios supplied with 4 colonies per hectare it was  $31.5 \pm 8.6$  US\$/ha (mean  $\pm$  SE).

However, on closer analysis of the results, the decision to use a density of 8 colonies per hectare of crop was more profitable in apple orchards with an area of less than 100 cultivated hectares ( $\approx 13\%$  of the total landscape), in which context the performance was superior to that of the investment using 4 colonies per hectare. On the other hand, in apple orchards that exceeded 100 cultivated hectares, it was observed that using a density of 4 hives per hectare of crop was a more efficient and profitable investment than using a higher density of colonies (Fig. 7).

## 4. Discussion

Honey bee pollination services directly impact the productivity of many important crops that require these services for their viability. Applying the model of Joseph et al. (2020) in real agricultural landscapes, we have demonstrated that colony density has a positive effect on the number of visits to the crop, but this does not always ensure a higher number of pollinated flowers. Our results show that higher colony density can increase the number of pollinated flowers per hectare only up to a point, since when the cover of apples  $\geq 40\%$  of landscape area, increasing honey bee density through the introduction of a large quantity of colonies does not necessarily ensure higher flower pollination (Fig. 5b). These results have strong implications for the management practices of crop pollination, providing information on how to maximize pollination services.

We found not only a decrease in the number of pollinated flowers per hectare of the target crop at the highest colony density, but also an increase in the number of visits to the surrounding landscapes, mainly mass-flowering crops and the natural habitats; this is due to the increasing cover of apple crops and the resulting higher density of honey bee colonies in the crops (Appendix D). This increase in the number of visits to the landscape is the result of redistribution of honey bee foragers in search of new foraging sites, due to a decrease in the availability of resources in the targeted crop because of high honey bee densities and the consequent increase in competition among foragers. Moreover, this change in the spatial distribution of honey bee foragers was modulated by the blooming period and relative attractiveness of floral resources in each land cover class (Riedinger et al., 2014). This spillover mechanism of the honey bee foragers from the crops to the adjacent habitats has been surprisingly under-researched, even though it is very likely to occur frequently in productive landscapes (Dicks et al., 2010; Blitzer et al., 2012; Tschamtko et al., 2012; Holzschuh et al., 2016; Osterman et al., 2021).

Our results show that the landscape complexity that surrounds the target crop fields moderates the distribution of pollinators in productive landscapes. This is because an increase in cover of mass-flowering crops and natural habitats generates a decrease in the number of visits to the crop, especially when colony density is high. Colony densities were greater in landscapes with high cover of apple crops, which led to higher densities of honey bees in nearby habitat patches. When blooming, apple crops acted as an attractant for honey bees, reducing their densities in nearby habitat patches. However, a sizeable honey bee spillover from apple crops into adjacent habitats occurred before and after crop bloom. While blooming, apple crops can retain to some extent the hive-mediated surplus of foragers on a landscape scale. However, this transient attraction effect turned into a massive spillover effect in periods before and after the blooming of apple crops, resulting in higher visitation rates in other habitats that provide food resources, mainly other mass-flowering crops (cherries, blueberries, etc.) and natural habitats (Appendix E). This spillover was resource-mediated, since it happened at the same time as a sudden shortage in floral resources in apple crops. These results are consistent with the theoretical predictions of the cross-habitat spillover of mobile organisms across the managed-natural system interface (Blitzer et al., 2012; Tschamtko et al., 2012), and previous studies that document such effects in oilseed rape (Holzschuh et al., 2011) and orange groves (González-Varo and Vilá, 2017).

The spatially explicit model presented in this work provides a valuable insight into the efficiency of different management strategies and the effects of landscape composition and configuration on crop pollination with managed honey bee colonies. This represents an opportunity to improve crop productivity through better management of pollinators. In our analysis, we have shown a positive effect of honey bee densities on crop visitation rates. However, this relationship seems to be nonlinear for the number of pollinated flowers. In this context, increasing the number of colonies in the landscape, and consequently, the number of honey bee foragers, does not necessarily signify a proportional increase of honey bee foragers in the targeted crop, or higher pollination. In fact, stocking a field with more colonies does not necessarily result in higher fruit production (e.g., Viana et al., 2014). Our results have direct implications for farmers' profits. We estimated that the mean return on investment for farmers, averaged across all apple orchards studied, was 29.3 US\$ for the high colony density, and 31.5 US\$ for the low colony density. Comparing across management strategies, the best return of investment outcomes was gained with a low colony density (4 cph), except in smaller apple orchards ( $< 100$  ha), where the most efficient strategy proved to be high colony density (8 cph). This finding is positive for farmers, because routine management practices in bee pollination uses the honey bee colony as a management unit, with beekeeper and farmer agreeing on a rental price per colony. Therefore, our model can help guide decision making regarding the number of colonies needed to increase the efficiency of pollination activity at the

lowest possible cost.

It is important to note that our assumption that the values of the number of visits per flower needed to ensure full ovule fertilization are homogeneous for all land-cover types is an extrapolation. The model input parameters are based on values that are still unclear for most crops, so sufficient data are not always available to parameterize the model. Consequently, we recommend validating the model against observational data to ensure its predictions reflect current observed reality. Another factor to consider is the estimation of floral attractiveness based on expert opinion. Experts scored land-cover types independently, so expert opinion scores may be inaccurate or not yield the most appropriate values within our modeling scenario. A more sophisticated elicitation method may have provided more reliable final scores, allowing the experts to collectively review all opinions and iteratively refine and discuss their scores (Gardner et al., 2020). Finally, management recommendations are highly variable, with strong fluctuations depending on the crop, cultivar and spatial context. Therefore, we recommend building the modeling scenarios according to the local pollination strategies to be evaluated.

Maximizing production and reducing yield gaps in pollinator-dependent crops are key challenges with strong implications for farmers and consumers worldwide (Garibaldi et al., 2016). The model presented here can serve as a useful tool to assess the effectiveness of current pollination practices, and could be used to improve pollination practices in different applied contexts. Based on our model results, improving pollination through effective management can have a potentially large economic effect on farmers' income. Furthermore, as the model can handle cases of resource supplementation (Tschamtko et al., 2012), it can provide important insights into the mechanisms driving the occurrence and magnitude of honey bee spillover; namely, temporal changes in floral resources on local and landscape scales, and increased beekeeping on a landscape scale (both to provide pollination services to crops and produce honey). Given that in some places pollinators are managed at densities that are higher than optimal, we expect that this model can help guide local management decision making and result in more limited spillover (Garibaldi et al., 2017) of managed pollinators from crop areas into natural areas, thus reducing their potentially detrimental effects (Goulson, 2003; Herbertsson et al., 2016; Vanbergen et al., 2018).

**CRedit authorship contribution statement**

**Fernanda Santibañez:** Conceptualization, Methodology, Software, Investigation, Formal analysis, Writing – original draft, Visualization. **Julien Joseph:** Methodology, Software, Investigation, Formal analysis, Data curation, Writing – review & editing. **Guillermo Abramson:** Methodology, Software, Investigation, Writing – review & editing. **Marcelo N. Kuperman:** Methodology, Investigation, Writing – review & editing. **María Fabiana Laguna:** Methodology, Investigation, Writing – review & editing. **Lucas A. Garibaldi:** Conceptualization, Methodology, Investigation, Formal analysis, Writing – review & editing.

**Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

**Data availability**

The authors are unable or have chosen not to specify which data has been used.

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**Appendix A**

Table A1

Table A.1

Blooming period and floral attractiveness (FA) scores for the land-cover types. In this work we consider that the resource carrying capacity per cell is 7 g; this is constant during the blooming period and equal to zero for the rest of the year. The daily resource renewal rate is 100%. See Joseph et al. (2020) for further information.

LULC Code	Description	Blooming period	FA
1	Other annual crops	0 – 130	0.4
2	Apples	10 – 40	0.9
3	Pears	5 – 35	0.9
4	Hazelnuts	110 – 140	0.9
5	Blueberries	25 – 55	0.9
6	Raspberries	5 – 35	0.9
7	Blackberries	55 – 85	0.9
8	Cherries	0 – 30	0.9
9	Kiwis	60 – 90	0.9
10	Nuts	5 – 35	0.9
11	Olives	45 – 75	0.4
12	Natural and semi-natural habitats	0 – 182	0.75
13	Water courses and water bodies	–	–
14	Urban areas	0 – 182	0.05
15	Bare rocks	–	–
16	Glaciers and perpetual snow	–	–

**Appendix B**

Table B1

Table B.1

Summary of the main parameters used in the model. We used a set of parameters that corresponds to the region of Maule (Chile). Colony life history has been modeled following Khoury et al. (2013).

Description	Symbol	Value	Units	References
Map size		3	km	
Cell size		10	m	
Time step		1	day	
Flowering period		30	days	(Lesser Preuss, 2004)
Flowers per cell		15,000		(Lesser Preuss, 2004)
Daily renewal rate of the resource	$r$	100%		adjusted
Resource carrying capacity per cell	$K$	7	g	(Křevska et al., 1995; Lesser Preuss, 2004)
Knowledge of the environment	$\gamma$	3		adjusted
Size of squad	$k$	200		arbitrary
Trips per forager per day	$N_{trips}$	19		(Hagler et al., 2011)
Flower visited in one forager's trip	$N_{flower,trip}$	75		(Hagler et al., 2011)
Maximum foraging distance	$r_f$	3	km	(Abou-Shaara, 2014)
Maximum food a forager can bring back on one trip	$c$	0.1	g	(Khoury et al., 2013)
Constant decay rate	$\lambda$	-0.029		(Sáez et al., 2018a)
Mean efficiency of one visit	$p$	0.75		(N. Vicens and Bosch 2000; Rollin and Garibaldi, 2019)

Appendix C

Table C1

Table C.1

Best models as ranked by AIC ( $\Delta AIC (\Delta_m) < 4$ ). Each row represents one model and columns provide information about each model. Plus and minus signs indicate whether the estimates of the effects (columns) of predictors in each model were positive or negative, respectively. Shaded cells indicate that effect (column) is not included in the model (row). The relative importance (ri) of each predictor is informed in the last row.

Apple crops											
No. visits per hectare ( $\Delta AIC (\Delta_m) < 4$ ; AIC best-ranked model = 7235.6)											
Rank	<i>ln(apple)</i>	<i>ln(apple)<sup>2</sup></i>	<i>density</i>	<i>distance</i>	<i>MFC cover</i>	<i>SNH cover</i>	<i>ed land</i>	<i>density: ln(apple)</i>	<i>density: ln(apple)<sup>2</sup></i>	<i>distance: ln(apple)</i>	$\Delta_m$
1	+		+		-	-	-	+			-
2	+		+		-	-	-	+			1.33
3	+		+	-	-	-	-	+			1.96
4	+		+	-	-	-	-	+			3.29
5	+		+	-	-	-	-	+		+	3.96
<i>ri</i>	<b>1</b>	<0.01	<b>1</b>	0.34	<b>1</b>	<b>1</b>	<b>0.66</b>	<b>1</b>	<0.01	<b>0.09</b>	
No. pollinated flowers per hectare ( $\Delta AIC (\Delta_m) < 4$ ; AIC best-ranked model = 6032)											
Rank	<i>ln(apple)</i>	<i>ln(apple)<sup>2</sup></i>	<i>density</i>	<i>distance</i>	<i>MFC cover</i>	<i>SNH cover</i>	<i>ed land</i>	<i>density: ln(apple)</i>	<i>density: ln(apple)<sup>2</sup></i>	<i>distance: ln(apple)</i>	$\Delta_m$
1	+	-	+		-	-	-	+	-		-
2	+	-	+	-	-	-	-	+	-		1.95
3	+	-	+	-	-	-	-	+	-	+	3.94
4	+	-	+	-	-	-	-	+	-	+	3.95
<i>ri</i>	<b>1</b>	<b>1</b>	<b>1</b>	0.41	<b>1</b>	<b>1</b>	<b>0.97</b>	<b>1</b>	<b>1</b>	<b>0.03</b>	
Surrounding landscape											
No. visits per hectare ( $\Delta AIC (\Delta_m) < 4$ ; AIC best-ranked model = 6586.4)											
Rank	<i>apple cover</i>	<i>apple cover<sup>2</sup></i>	<i>density</i>	<i>distance</i>	<i>MFC cover</i>	<i>SNH cover</i>	<i>ed land</i>	<i>density: apple</i>	<i>density: apple<sup>2</sup></i>	<i>distance: apple</i>	$\Delta_m$
1	+	+	+		+	+		+	+		-
2	+	+	+		+	+	-	+	+		1.79
3	+	+	+	+	+	+		+	+		1.99
4	+	+	+	+	+	+	-	+	+		3.79
5	+	+	+	+	+	+		+	+		3.99
<i>ri</i>	<b>1</b>	<b>1</b>	<b>1</b>	0.36	<b>1</b>	<b>1</b>	0.29	<b>1</b>	<b>1</b>	<b>0.12</b>	
No. pollinated flowers per hectare ( $\Delta AIC (\Delta_m) < 4$ ; AIC best-ranked model = 5749)											
Rank	<i>apple cover</i>	<i>apple cover<sup>2</sup></i>	<i>density</i>	<i>distance</i>	<i>MFC cover</i>	<i>SNH cover</i>	<i>ed land</i>	<i>density: apple</i>	<i>density: apple<sup>2</sup></i>	<i>distance: apple</i>	$\Delta_m$
1	+	-	+		+	+		+	-		-
2	+	-	+		+	+	-	+	-		1.83
3	+	-	+	+	+	+		+	-		1.98
4	+	-	+	+	+	+	-	+	-		3.82
5	+	-	+	+	+	+		+	-	-	3.98
<i>ri</i>	<b>1</b>	<b>1</b>	<b>1</b>	0.36	<b>1</b>	<b>1</b>	0.29	<b>1</b>	<b>1</b>	<b>0.12</b>	



Appendix D

Fig D1

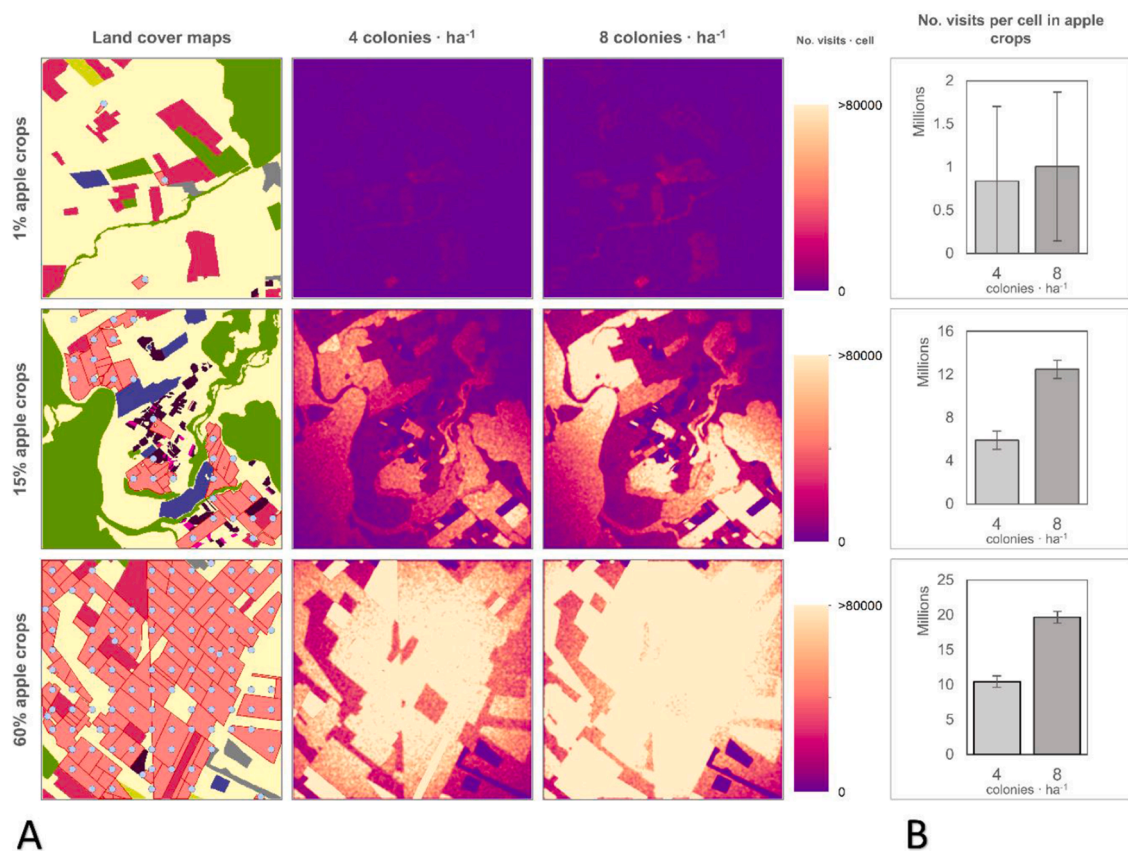


Fig. D.1. The output matrix of the average number of visits per cell generated by the model. The top row shows the landscape sampling unit with the minimum percentage of apple crops (0.47%), the middle row shows the landscape sampling unit with the average percentage of apple crops (14.47%), and the bottom row shows the landscape sampling unit with the maximum percentage of apple crops (60.6%). The plots on the right side of the figure show the average number of visits per cell in apple crops for each colony density.

Appendix E

Fig E1

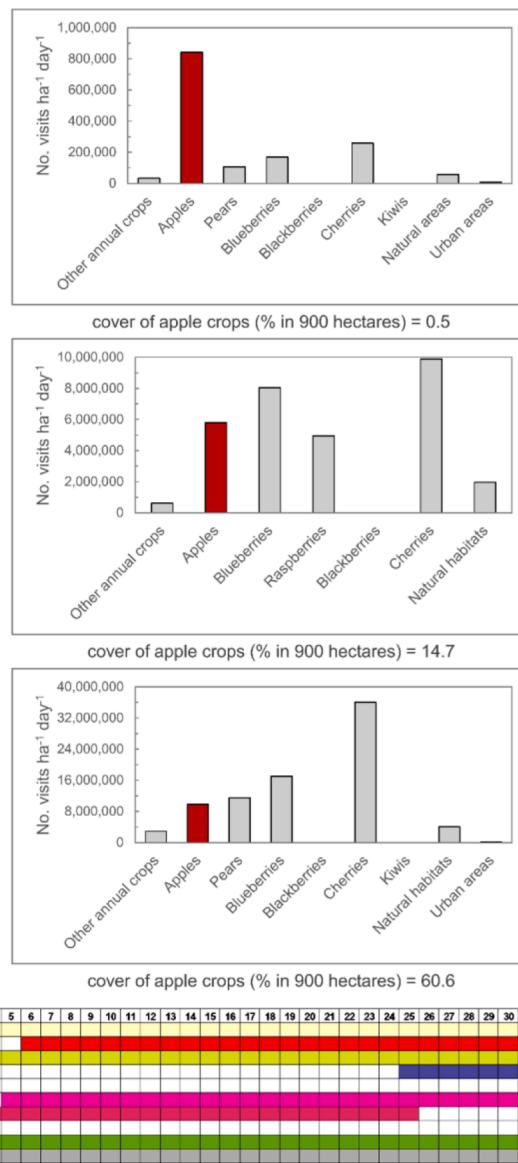


Fig. E.1. Analysis of the number of visits and flowering calendar for different land-cover types. Top: 1% of the landscape corresponds to apple crops. Middle: 15% of the landscape corresponds to apple crops. Bottom: 60% of the landscape corresponds to apple crops. Before and after blooming in the apple orchards, honey bees must forage in the surrounding landscape.

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