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RESEARCH ARTICLE

Landscape structure and farming management interacts to modulate pollination supply and crop production in blueberries

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Abstract

1. Pollination services are affected by landscape context, farming management and pollinator community structure, all of which impact flower visitation rates, pollen deposition and final production. We studied these processes in Argentina for highbush blueberry crops, which depend on pollinators to produce marketable yields.
2. We studied how land cover and honeybee stocking influence the abundance of wild and managed pollinators in blueberry crops, using structural equation modelling to disentangle the cascading effects through which pollinators contribute to blueberry fruit number, size, nutritional content and overall yield.
3. All pollinator functional groups responded to landscape changes at a spatial scale under 1000 m, and the significance or direction of the effects were modulated by the field-level deployment of honeybee hives.
4. Fruit diameter increased with pollen deposited, but decreased with honeybee abundance, which, had indirect effects on fruit acidity. Honeybees had a positive effect on the number of fruit produced by the plants and also benefited the overall yield (kg plant^{-1}) through independent effects on both the quality and quantity components of fruit production.
5. *Synthesis and applications*. Deployment of beehives in blueberry fields can buffer, but not compensate for the negative effects on honeybee abundance produced by surrounding large scale none-flowering crops. Such compensation would require high-quality beehives by monitoring their health and strength. The contribution of honeybees to crop production is not equal across production metrics.

That is, higher abundance of honeybees increases the number of berries produced but at the cost of smaller and more acidic fruits, potentially reducing their market value. Growers must consider this trade-off between fruit quantity and quality when actively managing honeybee abundance.

KEYWORDS
beehive, fruit quality, honeybee, landscape, pollen deposition, *Vaccinium*, yield

1 | INTRODUCTION

Management of pollination services is frequently based on introducing honeybee hives in production systems (Rollin & Garibaldi, 2019). Recommendations of stocking densities are highly variable and focus on hive numbers instead of target flower visitation rates (Garibaldi et al., 2020). Typically, growers saturate crops with honeybees while ignoring wild pollinators (DeVetter et al., 2022) or give little consideration to how surrounding landscape interacts with farm management and impact the provision of pollination services (Garibaldi et al., 2017). Furthermore, because the relationship between pollinator-centred (e.g. diversity, abundance or visitation rate) and plant-centred metrics (e.g. seed and fruit set, fruit quality or yield) can vary substantially (Bartholomée & Lavorel, 2019), the contribution of pollinators to one production metric may not be generalisable to the others. Since not all production metrics are of equal relevance for growers, it is essential to understand how pollination services influence and contribute to the different aspects of the production. Such understanding requires a systemic approach to investigate how landscape and farm management affect the abundance of pollinators (Tscharntke et al., 2012), which will affect the flower visitation rates (Garibaldi et al., 2013), field-level pollen deposition (Shaw et al., 2020) and ultimately the different aspects of crop productivity (Garibaldi et al., 2019).

The Southern highbush blueberry (*Vaccinium corymbosum* L.) is a mass-flowering crop that is highly dependent on animal pollination to produce marketable yield (Reilly et al., 2020). Although the study of landscape factors explaining pollination service delivery in blueberries have received considerable attention (Benjamin et al., 2014; Cavigliasso et al., 2022; Nicholson et al., 2017), the effect of the interaction between spatial patterns and local pollination management are still unclear (Eeraerts et al., 2022). Regional pollinator abundance is strongly influenced by the intensity of agricultural activities (Nicholson et al., 2017), the amount and arrangement of resources in the landscape (Santibañez et al., 2022) and functional attributes of the pool of pollinators (Westphal et al., 2006). While the role of landscape heterogeneity has been widely documented for wild species, its impact on honeybees is often overlooked. Large-scale mass flowering crops dilute honeybee flower visitations (Tscharntke et al., 2012), resulting in complex responses to landscape depending on crop area (Isaacs & Kirk, 2010) and pollination management (Mallinger et al., 2021). Blueberry growers use predetermined pollinator densities to increase the stability of pollination services throughout the bloom period (MacKenzie, 1997), regardless of landscape context. However, recommendations on beehive density vary greatly and can range between 0 and 40 colonies per hectare (DeVetter et al., 2022; Rollin & Garibaldi, 2019), but the effects on the flower visitation rate (Cavigliasso et al., 2021; Eeraerts et al., 2022) or crop production (Cavigliasso et al., 2021; Mallinger et al., 2021) are highly variable. Hence, succeeding in avoiding pollination shortfalls depends on integrating the study of the effect of landscape and local management of pollinators.

The total contribution of pollination to crop productivity results from the interaction between pollinators identity, pollen transfer and several production dimensions. In the case of blueberries, the overall yield, the quality or size of individual fruits, and the taste determine the market value (Argentine Ministry of Agroindustry 2015—resolution SAGyP N° 201/2007). The relationship between flower visitation rate and each of these production metrics is not easily predictable as it depends on the pollination variable (e.g. hive density or honeybee visitation rate, see Mallinger et al., 2021), pollinator type (Isaacs & Kirk, 2010; Nicholson & Ricketts, 2019) and blueberry cultivar (Kendall et al., 2020; Ramírez-Mejía, Lomáscolo, et al., 2023). Therefore, gains in fruit diameter resulting from an increased frequency of pollinator interactions may not directly translate in higher crop yield (Ramírez-Mejía, Lomáscolo, et al., 2023). Similarly, higher fruit set does not necessarily imply higher fruit quality (i.e. size and nutritional content, see Cavigliasso et al., 2020). These complex patterns suggest that the pollination effect in one production metric is not directly transferable to another, which highlights the need for an integrative approach to maximise the net production gain. For example, promoting a fruit set of ~70% in blueberries requires ~5.5 less pollen deposition (Drummond, 2019) than needed to produce high-quality fruits (Dogterom et al., 2000). While three to five visits are sufficient to increase the probability of flowers setting fruit to 0.9, 15 visits are required to increase fruit size (Kendall, 2020). Understanding how different pollinators can meet such pollen demand (Barcala et al., 2021), and the potential trade-offs and cascading effects that affect multiple production metrics, would improve our ability to predict the contribution of animal pollination to overall crop production.

In this study, we link landscape, on-farm pollinator management, flower visitation, pollen deposition and various aspects of blueberry production to answer two complementary questions: (i) How do spatial scale, landscape variables and local pollinator management interact to modulate the abundance of wild and managed pollinators in blueberry crops? (ii) How do such pollinators contribute to the quality and quantity of blueberry production, through cascading effects involving frequency of flower visitation, pollen deposition and final overall production?

2 | MATERIALS AND METHODS

2.1 | Study system

The study was conducted in the province of Tucumán (26° 50′ 02″ S, 65° 12′ 55″ W), Argentina. This landscape transitions from primary and secondary subtropical Andean forest in the mountain foothills to the west (Appendix S1, Figure S1a), to heavily deforested agricultural land dominated by plantations of citrus, sugarcane and soybean fields (Appendix S1, Figure S1a). Blueberries occupy only a small fraction of the cultivated area, with farms usually adjacent to citrus orchards, or in areas with sugarcane or soybeans. Our study system consists of nine blueberry farms surrounded by different landscape contexts and subject to different pollination management practices (Appendix S1, Figure S1a). Farms ranged in size from 10.1 to 70.7 ha ($M=39.6\pm20.9$ SD) and were separated by an average of 9.5 ± 2.4 km (Appendix S1, Figure S1a). We assessed a single blueberry cultivar (Emerald), which is one of the most widespread in this region (Association of Blueberry Producers, pers. com.). This cultivar is self-compatible and, in the absence of animal pollination, can produce a delayed harvest of small berries with significantly lower economic value (Müller et al., 2013).

2.2 | Landscape and management factors modulating pollination service

2.2.1 | Sampling design and pollinator observation

In total, we sampled pollinators on nine farms, eight in 2020 and six in 2021—five of these farms were sampled in both years. Five farms had honeybee hives to enhance crop pollination while four rely on wild pollinators or feral honeybees (Appendix S1, Figure S1a). On each farm, we established an edge area (25 m from the field margin) and an inner area (50 m from the field margin), each comprising two 70 m transects running parallel to the field margin and separated by 8 m. On each of the four transects we selected 25 plants in full flower on which we conducted three 30-s pollinator counts, one in the morning, one at midday and one in the afternoon. All sampling took place between 10:00 and 17:00 on sunny days with low wind and a temperature above 15°C. We recorded the abundance of honeybees, small wild bees—any bee smaller than a honeybee—hoverflies (Syrphidae) and butterflies. Hummingbirds and large wild bees (bumblebees *Bombus* spp. and carpenter bees *Xylocopa* spp., which are all larger than honeybees) showed behaviours that made them difficult to record as they fled when surveyors approached the plants. Therefore, after every 25 plant pollinator counts, we walked the same transect to record the abundance of hummingbirds and large wild bees for 5 min. This sampling protocol was repeated twice for each farm in each year (2020 = 56 h, 2021 = 42 h of pollinator counts).

2.2.2 | Landscape classification

All land use classifications were carried out using the interactive Google Earth Engine application 'Your Maps Your Way' (Morton & Schmucki, 2023). A detailed explanation of the classification process can be found in Appendix S1, Table S1. In summary, we classified the different land covers into three broad categories: (i) natural cover (natural primary forest, secondary forest and shrubland), (ii) flowering crops (citrus and blueberry) and (iii) large-scale crops (sugarcane and soybean crops). We grouped flowering crops together because blueberries occupy a small area compared to citrus, although both are perennial and provide comparable resources (Emerald bloom in August and citrus in September). We used the *terra* (Hijmans, 2022) and *sf* (Pebesma, 2018) R packages to define the area of the three land use classes within concentric circles with a radius of 200 to 4000 m around each site, progressively increasing the radius by 200 m (Appendix S1, Figure S1a). This was done to identify the spatial scale of pollinator responses to land use.

2.2.3 | Statistical analysis

This analysis aimed to evaluate the effect of scale, landscape metrics and local pollination management on pollinators abundance within the crops. We established four sets of models examining the abundance of (i) honeybees, (ii) hummingbirds, (iii) large wild bees and (iv) small wild pollinators (small wild bees, hoverflies and butterflies). For each response variable, we fitted generalised linear mixed models (GLMM) using one land cover variable interacting with pollination management factor as a fixed effect (two levels, use or non-use of beehives), and time of day nested within the farm as a random effect (Appendix S1, Table S2). These models were repeated in 200 m increments for each spatial scale from 200 to 4000 m. To include a predictor that encompasses the joint effect of all landscape variables (natural cover, flowering crops and large-scale crops) we applied a principal component analysis at each of the 20 spatial scales and used the first component (PC1) axis scores. By ranking models based on the highest marginal R^2, we identified the spatial scale and landscape predictor that best explained the abundance of each pollinator functional group (see Appendix S1, Table S2 for more details).

2.3 | Cascading effects: From pollinators to production

This analysis aims to investigate cascading processes involving pollinators with final effects on blueberry production. During the 2021 flowering season (July–August), we used a subset of the nine farms ($N=3$) to examine the effects of pollinators on blueberry pollen deposition and productivity metrics. On these farms growers manage pollination services using honeybee hives. On each farm, we selected five to six plots (Emerald cultivar, plot size 1.31 ± 0.09 ha) distributed from the edge of the farm to the interior to capture the potential variation in underlying pollination services, soil condition, irrigation system and plant age (Appendix S1, Figure S1b). The average distance between plots was 384.4 ± 197.5 m. In each plot, we randomly selected five plants and conducted a 5-min pollinator count per plant under the same weather conditions as mentioned above (26.6 ± 2.8 plants per farm). Previously, we estimated the floral display size per plant by combining the flowering percentage of the plant, the total fruits produced (see Section 2.3.2) and the fruit set of the Emerald cultivar at each farm (see the detailed procedure in Appendix S1, Table S3). We recorded the abundance of honeybees and small wild pollinators. We also used the plant as a central point to record the abundance of hummingbirds and large wild bees in an area of 12 m^2 (area occupied by 14 blueberry plants). The density of honeybee hives within 200 m (12.5 ha) of each sampled plot was recorded (Appendix S1, Figure S1b). Each plant was sampled twice during the ~30 day flowering period (13.3 h of pollinator observation).

2.3.1 | Pollen deposition

After flower anthesis, we collected three styles per plant from senescent flowers (N_{total} = 240). These were placed on a microscope slide after a transversal cut of the style at the stigma height and stained with Alexander's solution (Alexander, 1969). We then counted the number of pollen grains as a measure of the stigmatic pollen load.

2.3.2 | Production metrics

We considered the following metrics to assess the quality and quantity of blueberry production: (1) We visited each sampled plant and counted the total number of fruits on two randomly selected primary branches. The product of the average number of fruits per primary branch and the number of primary branches was used as an estimate of the total number of fruits per plant. (2) We randomly selected 10 mature fruits per sampled plant and measured their equatorial diameter. (3) Plant yield (kg $plant^{-1}$) was the product of average fruit weight ($N_{fruits\ per\ plant}$ = 10) and the total number of fruit produced. (4–7) Nutritional content based on a 30 g fruit sample in the form of degrees Brix (measure of sugar content), total acidity and concentration of anthocyanins (Appendix S1, Table S4 for the laboratory protocol).

The fieldwork and data collection in blueberry farms were conducted in agreement with farmers; no further ethical approval or legal permission was required.

2.3.3 | Statistical analysis

Using structural equation modelling (SEM), we evaluated the effects of pollinators on blueberry pollen deposition and the resulting effects on production metrics. As the data structure was nested (blueberry plants nested within plot and farm), we applied a generalised multilevel path analysis (*picewiseSEM* R package) (Lefcheck, 2016). First, we defined a conceptual model of variable relationships based on the sequential steps of the pollination service process (Figure 1). A detailed explanation of the conceptual model can be found in Appendix S1, Table S5.

We then defined each equation in the SEM as a GLMM using the plot nested within the farm as a random effect (R package *nlme*, Pinheiro et al., 2022). Predictors (or response variables depending on the equation) were floral display size, beehive density and abundance of honeybees, hummingbirds/large wild bees and small wild pollinators. We combined the data of hummingbirds and large wild bee because of the large number of zeros—about 80% for hummingbirds. We also included stigmatic pollen load and its coefficient of variation, fruit diameter, number of fruit produced per plant, plant yield, fruit acidity, degrees Brix and anthocyanins content. The equation (i.e. model) assessing the effect of pollinators on the fruits produced per plant, was conditioned by the floral display size. We use *Shipley' test of direct separation* and *Fisher's C* to assess the goodness-of-fit of the model (Shipley, 2000). A *p*-value of >0.05 means that there is no significant difference between the observed and estimated variance–covariance matrix and thereby a good model fit.

3 | RESULTS

3.1 | Landscape and management factors modulating pollination service

Honeybees accounted for 97.6% (±SD 1.9) of the total records and were 48 times more abundant than small wild pollinators. For the larger pollinators, 60.6% were hummingbirds and 39.3% were large wild bees. In general, all functional groups of pollinators responded to landscape variation at a spatial scales under 1000 m.

Honeybee abundance was negatively affected by large-scale crops within 800 m radius (Appendix S2, Figure S1a). This negative effect was 2.8 times stronger when farmers did not use managed beehives (Figure 2a) and the explained variance decline substantially at 1800 m, followed by a gradual increase up to 4000 m (Figure 2a). The model fitted at 800 m radius explained 64.4% of the total variation in honeybee abundance (marginal R^2 = 36.7%, Appendix S2, Table S1 and Figure S1). The model residuals meet normality assumptions (Appendix S2, Figure S2).

Hummingbirds abundance was mainly influenced by the joint effect of the landscape variables (i.e. PC1) measured within 800 m radius, with an abrupt drop at 1200 m (Figure 2b; Appendix S1, Figure S1c). At the 800 m scale, the increase along PC1 was associated with decline in the area of flowering crops (Appendix S2, Figure S3). The PC1 had a positive effect on hummingbirds abundance when farmers did not use managed beehives, but the effect was negative when beehives were present (Figure 2b; Appendix S2, Table S1). The 800 m radius model explained 52.4% of the variation in hummingbird abundance (marginal R^2 = 47.4%;

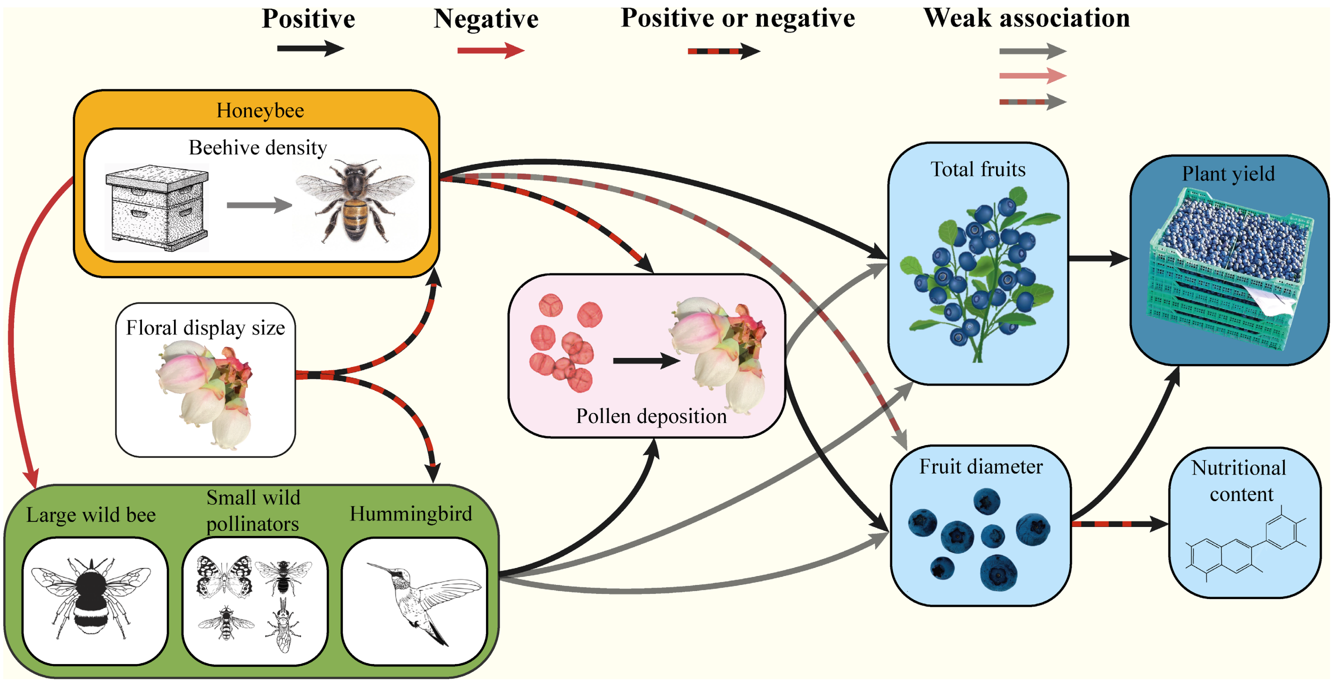

FIGURE 1 Conceptual model showing hypothetical paths through which pollinators affect pollen deposition and metrics of blueberry productivity (Appendix S1, Table S5). The combination of fruit diameter and total fruits results in the final plant yield. Credits of black and white pollinator images: www.divulgare.net.

Appendix S2, Figure S3). The model residuals meet normality assumptions (Appendix S2, Figure S3).

The abundance of small wild pollinators was mainly influenced by the area of flowering crops measure at 200 m scale (Appendix S2, Figure S1; Figure 2c). This effect was significantly negative, regardless of the presence of honeybee hive on the farm, but the relationship was 0.4 stronger in farms using beehives (Figure 2c; Appendix S2, Table S3). The 200-m model explained 36.2% of the variation in small wild pollinators abundance (marginal $R^2=26.8\%$; Appendix S2, Figure S4). The model residuals meet normality assumptions (Appendix S2, Figure S4).

Large wild bees showed a clear response to the joint effect of landscape predictors (i.e. PC1) at a scale of 600 m (Appendix S2, Figure S1; Figure 2d). At this scale, increase along PC1 was related to decline in the area of flowering crop, and increase in the area of natural habitats and large-scale crops (Appendix S2, Figure S5). The abundance of large wild bees was negatively associated with PC1, but only on farms with managed beehives (Figure 2d). This model explained 52.9% of the total variation (marginal $R^2=25.5\%$, Appendix S2, Figure S5). The model residuals meet normality assumptions (Appendix S2, Figure S5).

3.2 | Cascading effects: from pollinators to production

The structural equation model showed that honeybees contributed most to pollen deposition and crop production. Their abundance was a function of the floral display size but was not influenced by beehive density at farm level (Figure 3). Increased honeybee abundance was also associated with higher variation in blueberry stigmatic pollen load, although this did not affect the average value for this metric (Figure 3). Increasing average stigmatic pollen load resulted in larger fruits with lower acidity. The effect of honeybees on fruit size or total number of fruits produced was not mediated by pollen deposition; instead, their abundance had direct negative effects on blueberry fruit size and positive effects on total number of fruits produced (Figure 3).

None of the pollination variables had a direct effect on yield (kg plant^{-1}), instead it was mainly explained by the number and size of fruits produced by the plant (Figure 3). The model was well-fitted and had no missing paths between the variables (global goodness-of-fit: Fisher's $C=98.36$; p-value$\,=0.41$).

4 | DISCUSSION

Our study has two main findings: (i) the landscape context can interact with local pollination management and influence the abundance of pollinators on farms and (ii) the contribution of honeybees to blueberry productivity might imply trade-offs between the quality (i.e. fruit size and nutritional content) and quantity (i.e. number of fruits) components of the production. Indeed, this study shows evidence that the contribution of honeybees to crop yield is driven by independent effects on both the number and the size of fruits produced by the plants.

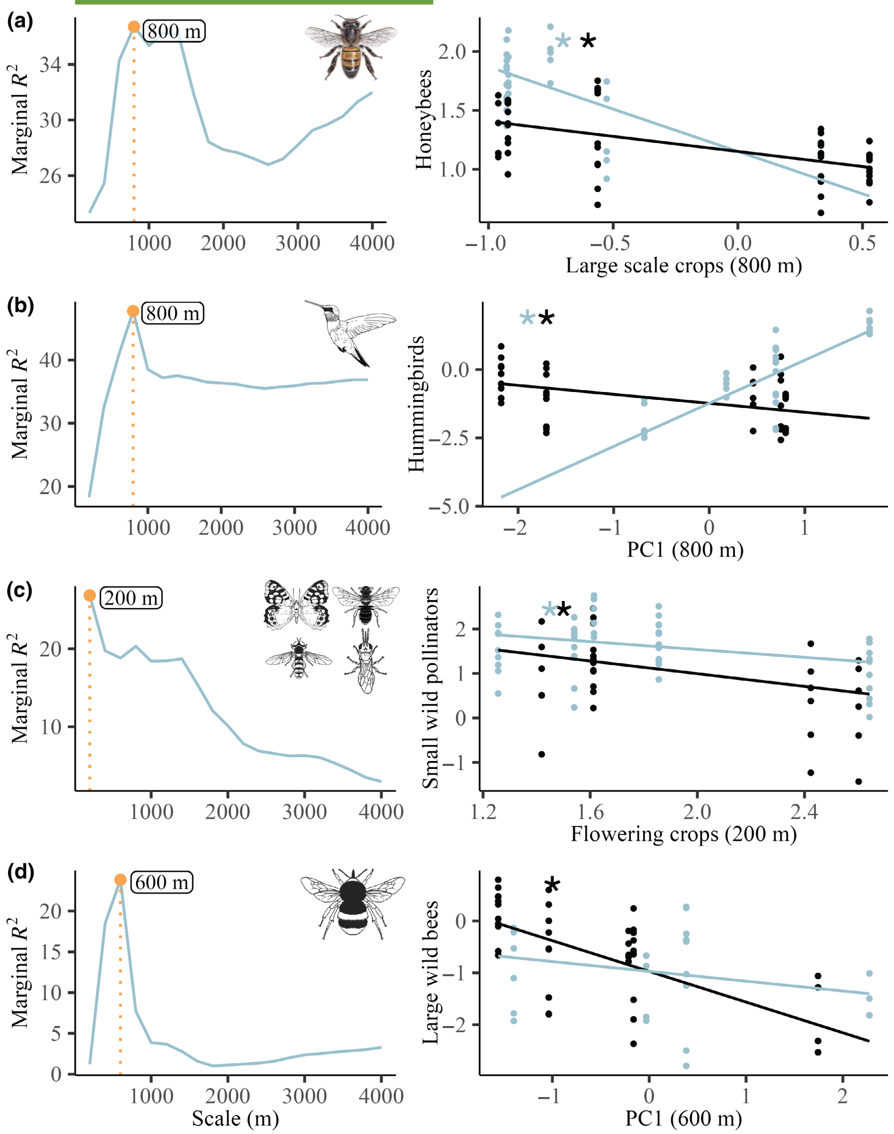

FIGURE 2 Scale of effect (left) and the main landscape predictor (right) explaining the abundance of honeybees (a), hummingbirds (b), small wild pollinators (c) and large bees (d). Panels on the left shows the marginal R^2 of generalised linear mixed models fitted at several landscape scales (200–4000 m), explaining changes in pollinator abundance as a function of the landscape predictor with the higher explanatory power (Appendix S2, Figure S1). The orange dote and vertical dotted line denote the spatial scale where the landscape predictor has the stronger effect on each pollinator functional group. Scatter plots of panels on the right correspond to the model with the higher marginal R^2 (i.e. orange dote in left panels). Black: farms using managed beehives; Light blue: farms without managed beehives. The asterisk denotes that the relationship is statistically significant for the trend line of the matching colour. In (b) and (d), the increase of PC1 corresponds to less area of flowering crops, higher natural area and large scale crops. Credits of black and white pollinator images: www.divulgare.net.

4.1 | Landscape and management factors modulating pollination service

Understanding the relationship between pollinators and the landscape is key for developing spatially explicit management strategies for pollination services (Santibañez et al., 2022). Body size is a strong predictor of bee foraging range (Greenleaf et al., 2007) and small pollinators are expected to respond to the landscape at a local scales—around 200 m (Ramírez-Mejía, Lomáscolo, et al., 2023). In contrast, larger species such as bumblebees and hummingbirds are more likely to utilise landscapes at larger spatial scales (Osborne et al., 2008; Tinoco et al., 2018). Honeybees can forage from hundreds of meters to ca. 10–12 kms from their hive (Beekman & Ratnieks, 2000), depending on landscape structure (Steffan-Dewenter & Kuhn, 2003), colony strength (Beekman et al., 2004) and resource requirements (Steffan-Dewenter & Kuhn, 2003). In our study, the main response of honeybees to the landscape was observed at 800 m, but effect was also detected at 1400 and 4000 m. This is consistent with honeybee-landscape relationship in other regions (Beekman & Ratnieks, 2000; Steffan-Dewenter & Kuhn, 2003), and probably means that bees can use resources at different spatial scales (Beekman & Ratnieks, 2000). Interestingly, we found that the spatial effects varied with the presence of managed honeybee at the field level. Change in pollinator–landscape relationship may have three non-exclusive explanations: (i) counterintuitively, the abundance of honeybees on farms with no managed beehive was significantly higher than on farms with managed beehives (Appendix S2, Figure S5). This suggest that landscape-level honeybee population has a major role influencing field-level honeybee abundance (Eeraerts et al., 2022), which could be due to factors operating independently or synergistically. Low-quality hives used to pollinate the crops (Geslin et al., 2017), and the presence of feral populations of honeybees which may be more susceptible to large-scale crops when foraging. Our results, however, also show that introducing managed beehives on farms can reduces, but not fully compensate for the negative effects of surrounding large-scale non-flowering crops in honeybee abundance. (ii) Differences in honeybee abundance resulting from

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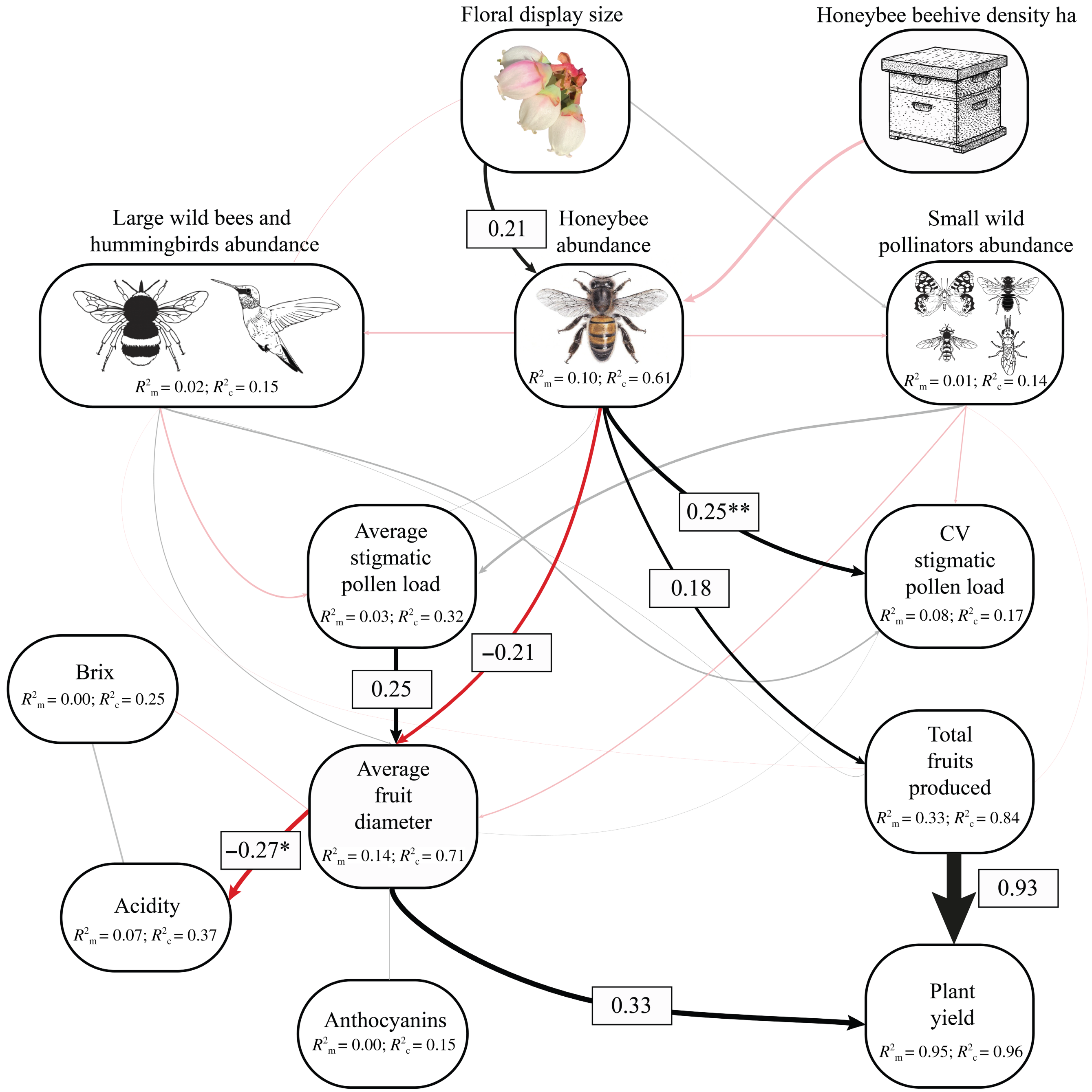

FIGURE 3 Structural equation model analysing direct and indirect effects of wild and managed pollinators on blueberry pollen deposition and production metrics. Boxes represent the variables measured and arrows denote unidirectional relationships. Black and red arrows represent, respectively, significant positive and negative effects. The numbers in boxes on each arrow denote the standardised regression coefficient. Arrow thickness is scaled by its standardised regression coefficient. Marginal and conditional R^2 are provided for each response variable in the structural equation system. Semi-transparent arrows denote non-significant relationships. The equation (i.e. model) explaining the effect of pollinators on total fruits produce, was conditioned by the floral display size of the plant (path not shown with $p<0.01$ and $\beta_{(standardised)}=0.47$). *$p=0.054$; **$p=0.055$. Credits of black and white pollinator images: www.divulgare.net.

the co-location of hives with crops can alter interspecific interactions between wild pollinators and their floral resources (Brittain et al., 2013; Eeraerts et al., 2020). This may directly affect the abundance of non-*Apis* pollinators and their response to the landscape (Miñarro et al., 2023). (iii) Finally, farm-level pollination management may mask other agricultural intensification practices (e.g. pruning of wild floral resources or use of pesticides) not considered in this study (Coutinho et al., 2018).

Natural and semi-natural habitats can increase the nesting survival of feral honeybees in agricultural landscapes (Rutschmann et al., 2022) and provide diverse nesting and floral resources for pollinators. Flowering crops, on the other hand, constitute abundant pulses of feeding resources that can boost wild pollinator populations when natural floral resources are scarce (Bänsch et al., 2020), such as winter season—which is the case of blueberry bloom at the Northwestern of Argentina. This landscape composition probably explains our findings: the negative effect of non-flowering large-scale crops on honeybee abundance, and the positive of flowering crops on hummingbirds and large bees. In contrast, the abundance of small insect pollinators was negatively affected by flowering crops. This is likely due to several factors including dilution effects as flowering resources increase (Santibañez et al., 2022), the attraction of adjacent citrus crops (Nicholson et al., 2019), the loss of non-floral nesting resources (Coutinho et al., 2018), or higher sensitivity to local farming practices.

4.2 | Cascading effects: from pollinators to production

Traditional management of pollination service is based on beehive stocking (Rollin & Garibaldi, 2019), which usually ignores colony strength and health (Geslin et al., 2017), as well as the contribution of feral honeybees to pollination (Eeraerts et al., 2022). Therefore, the relationship between hive density and honeybee activity is not clear (Mallinger et al., 2021). A prevalence of poorly managed beehives (Grant et al., 2021), could explain why we did not observe an increase in honeybee abundance with higher density of beehives.

Honeybee activity can influence pollen removal (Cunningham et al., 2016) and pollen deposition (Sáez et al., 2014) on flowering crops. Here, we report that increased honeybee abundance resulted in greater variability in stigmatic pollen deposition. This may be caused by excess visitations, resulting in stigmatic pollen removal or damage to the flower structures, which enhance variability in pollen deposition and reduce fruit quality (Aizen et al., 2014). Evidence of honeybee effects on blueberry fruit size is ambiguous; ranging from positive (Benjamin & Winfree, 2014; Isaacs & Kirk, 2010) to negative (Miñarro et al., 2023; Ramírez-Mejía, Lomáscolo, et al., 2023) or neutral relationships (figures 1 and 3 in Cavigliasso et al., 2021, but see Ramírez-Mejía, Lomáscolo, et al., 2023). Such variable evidence may stem from differences in the pollination dependence among cultivars (e.g. Ramírez-Mejía, Lomáscolo, et al., 2023). However, this could also result from density-dependent processes, where scenarios of deficit or over-pollination can occur at different locations. Evidence suggests a quadratic relationship between honeybee visitation and crop productivity for pollinator-dependent crops (Aizen et al., 2020; Rollin & Garibaldi, 2019). Therefore, neglecting target values for honeybee flower visitation in pollination management schemes may result in excessive visits that eventually reduce blueberry productivity. That is, the negative association, *production ~ honeybees*, found in this study and others (Mallinger et al., 2021; Miñarro et al., 2023; Ramírez-Mejía, Lomáscolo, et al., 2023) can result from over-pollination processes.

As expected, the importance of pollen deposition for blueberry production varies according to the production metric considered (quality: fruit size and nutritional content or quantity: number of fruits produced). Production of high-quality berries with a large equatorial diameter is more pollen demanding (Dogterom et al., 2000) than the production of large number fruits (Drummond, 2019). This explains why the frequency of pollinator interaction is more important than the quantity of pollen deposited for increasing the number of berries produced. Blueberry bushes of the cultivar we studied typically have ~5000 flowers. As such, increasing pollinator abundance in the field could increase the probability that each flower is visited at least once and thereby improve the overall fruit set. The trade-offs associated with increasing or decreasing honeybee interaction frequency within the crop are challenging. For example, we found that promoting field-level honeybee abundance would increase the number of fruits produced by the plants and the resulting yield, but in return the berries produced would tend to be smaller and have higher acidity levels. Quality production metrics, such as size (equatorial diameter) and nutritional content (sugar content), are valuable on the international market, as Argentinian blueberry growers are only allowed to export berries with a diameter of more than 12 mm and a sugar content above 7° Brix. Therefore, pollination management protocols should seek to balance the benefits of both the quality and the quantity of fruit production.

5 | CONCLUSIONS

Maintaining natural cover in the agricultural landscape benefits field-level activity of both wild pollinators and honeybees, but the effects can be contingent on the deployment honeybee hives within crops. Indeed, rather than the number of beehive per field, the abundance of feral honeybees measured at landscape-level might be more important for providing stable and efficient pollination services (Eeraerts et al., 2022). We encourage that, beyond hive density, blueberry growers monitor the strength and health of the colonies they deploy in their field to better predict the actual contribution of managed pollinators to crop productivity (Geslin et al., 2017). Moreover, management of pollinators abundance at the field-level using beehive should take into account potential trade-offs between the quantity and the quality of the fruit produced. That is, maximising the gains of particular production metrics might require different target levels of pollinator visitation. Therefore, the success of pollinator management in production systems depends on our understanding of crop requirement and the optimal pollination thresholds that will maximise the quality and quantity of the production.

AUTHOR CONTRIBUTIONS

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Andrés F. Ramírez-Mejía, Pedro G. Blendinger, Natacha P. Chacoff and Lorena Escobar. Land cover classification: Andrés F. Ramírez-Mejía, Richard Daniel Morton, Reto Schmucki. Analyses: Andrés F. Ramírez-Mejía with feedback from Ben A. Woodcock, Pedro G. Blendinger, Natacha P. Chacoff, Reto Schmucki. The manuscript was written by Andrés F. Ramírez-Mejía with critical review from Ben A. Woodcock, Pedro G. Blendinger, Natacha P. Chacoff, Reto Schmucki, Patrícia Nunes-Silva, Lorena Vieli, Silvia B. Lomáscolo, Maureen Murúa and Carolina Laura Morales. Pedro G. Blendinger and Reto Schmucki procured the funding.

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CONFLICT OF INTEREST STATEMENT

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. Ben A. Woodcock is an Associate Editor of Journal of Applied Ecology but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.bg79cnphc (Ramírez-Mejía, Blendinger, et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Nutritional content analyses, flowering display size estimations, and land cover classification.

Appendix S2. Models' outputs.

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