RESEARCH ARTICLE

Phenological overlap between crop and pollinators: Contrasting influence of native and non-native bees on raspberry fruits over the flowering season

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Abstract

1. Phenological overlap between crop flowering and pollinators is a crucial trait for the pollination of more than 75% of the world's crops. However, crop management rarely considers the seasonal aspect of plant–pollinator mutualism. Here, we investigate the phenological overlap between crops and pollinators and how it affects pollination and fruit production.

2. We measured the abundance and richness of native and non-native pollinators visiting raspberry flowers at two different times during the flowering season (i.e. early and late flowering periods) and examined their effects on crop yield in 16 fields.

3. The community of pollinators foraging on raspberry flowers was more diverse and dominated by native pollinators during the early flowering period when most native plant species were flowering. Later in the season, when native flower resources declined in the surrounding environment, raspberry flowers were visited mainly by two non-native bees: managed honeybees and the invasive bumblebee *Bombus terrestris*.

4. Pollinator contribution to raspberry yield was twice as high in the early flowering period compared to the late period (61% vs. 31% increase in drupelet set respectively). Flower damage caused by extremely high visitation frequencies by non-native bees in the late period was six times higher than in the early flowering period (30% vs. 5% of damaged flowers respectively).

5. *Synthesis and applications*. Providing sufficient pollen and nectar resources to support wild pollinators over extended periods in agricultural landscapes can contribute to crop pollination and ensure high fruit weight and quality. This can be achieved by restoring natural and semi-natural areas near crop fields with native, long-flowering plant species. Growers and crop breeding programmes should consider selecting flowering times that coincide with periods of high diversity or abundance of native pollinators to reduce dependence on managed pollinators.

1 | INTRODUCTION

Over the past 50 years, agriculture has become increasingly dependent on pollinators (Aizen et al., 2009), a process driven primarily by the disproportionate increase in the acreage of pollinator-dependent crops around the globe (Aizen et al., 2019). Creating and managing local habitats and surrounding landscapes to promote pollination services on agricultural land has been proposed as the most effective and environmentally friendly practice to enhance crop pollination (Garibaldi et al., 2014; Gemmill-Herren et al., 2021; Nowakowski & Pywell, 2016). However, the success of these practices requires that local pollinator communities are active when the target crop is flowering. A mismatch between the timing of crop flowering and pollinator activity may hinder pollen transfer, and thus adversely affect the yield of crops that depend on pollinators (Sritongchuay et al., 2021). For this reason, synchrony between pollinators and crop flowering is essential for effective pollination services (Sritongchuay et al., 2021). Despite its relevance, the effect of phenological overlap between pollinators and plants is rarely considered in crop and environmental management.

Landscapes are typically characterized by seasonality, with precipitation, temperature and daylight length being the main factors determining the flowering of plant communities (Amasino, 2010). The seasonality of plant flowering shapes the temporal availability of resources for flower visitors. From a coevolutionary perspective, a phenological synchronization between plants and their pollinators can be expected (Peralta et al., 2020). Furthermore, areas with higher plant species richness have been shown to support richer communities of pollinators (Ebeling et al., 2008). Likewise, the peak in pollinator numbers and diversity is expected to coincide with the flowering peak of the plant community (Ebeling et al., 2008; Escobedo-Kenefic et al., 2020). Conversely, pollinators are expected to decline when the abundance of foraging resources decreases (i.e. at the beginning or end of the flowering season), both in terms of abundance and the number of species (Ebeling et al., 2008; Escobedo-Kenefic et al., 2020). Therefore, if the community of native pollinators exhibits seasonal patterns of activity (Hirao et al., 2006), crops whose flowering phenology overlaps with that of local plant communities should benefit from a greater diversity of native visitors than crops that flower outside the flowering period of the local plant community.

The number and diversity of pollinators visiting a crop determine the quantity and quality of pollination, which can affect crop yield and the quality of the fruits and seeds produced (Albrecht et al., 2012; Garibaldi et al., 2013). For example, in a meta-analysis of pollination services in 41 cropping systems worldwide, Garibaldi et al. (2013) reported that increasing the number and diversity of wild pollinators increased production in all crops studied. However, pollination of many crops relies almost exclusively on managed pollinators, such as honeybees and some bumblebee species (Aizen et al., 2020; Garibaldi et al., 2013). In agricultural systems, the abundance and diversity of native pollinators visiting crops can vary in space and time because of different factors, including (a) management of key local and landscape habitats for native pollinators (Garibaldi et al., 2014), (b) competitive displacement of native pollinators due to an oversupply of managed bees or invasive pollinators (Aizen et al., 2020; Badano & Vergara, 2011) and (c) phenological overlap between crop flowering and the activity period of native pollinators (Sritongchuay et al., 2021). Changes in the abundance and diversity of pollinators delivering pollination services might indeed affect the cost–benefit ratio of plant–pollinator interactions and ultimately affect crop yield (Aizen et al., 2014). In particular, replacing an effective and diverse native pollinator community with a less effective and poor pollinator community—dominated by one or two managed or invasive non-native species—can increase interaction costs and, in turn, negatively affect crop yield (Aizen et al., 2020). For this reason, assessing crop flowering periods and how they synchronize with the phenology of local pollinator communities are essential aspects to consider when planning and managing cropping systems.

In raspberry (*Rubus idaeus*) crops, fruit quantity and quality increase when pollinators visit their flowers (Chagnon et al., 1991; Morales, 2009; Sáez et al., 2018). The numerous pistils of the multi-carpelled raspberry flower develop into drupelets if adequately pollinated. Pollinator visitation is necessary to fertilize most flower's ovules and ensure commercial-quality fruits (Cane, 2005; Sáez et al., 2018; Strelin & Aizen, 2018). In the absence of pollinators, raspberry fruits are misshapen due to incomplete ovule fertilization and therefore do not meet commercial standards (Cane, 2005; Morales, 2009; Sáez et al., 2018). Raspberry flowers are visited by many pollinators and the seasonality of their flowering period differs across varieties, with some cultivars having two flowering periods in the same year. These so-called remontant varieties are highly valued by growers as they produce more than one harvest per year. By producing flowers at two different times over the year, pollination of the early and late flowering periods is likely to rely on different assemblages of pollinators. This difference might affect pollination services and influence the quality and value of the raspberries. The two flowering periods of the remontant raspberry varieties make them an ideal model for investigating the impact of crop-pollinator phenological overlap and temporal changes in flower visitor abundance and identity on commercial fruit production.

Intermountain valleys on the eastern slopes of the Patagonian Andes, Argentina, present suitable conditions for raspberry cultivation. Autumn bliss, the leading raspberry variety in this region, is remontant. During the early flowering period, old canes that produced their first inflorescences the previous season and were subsequently

pruned have a second bloom in late spring. During this period (i.e. November–early December), most native plant species are blooming (de Groot et al., 2023; Forcone & Kutschker, 2006). In contrast, during the late flowering period, the new stems emerge from the rootstock and flower for the first time in late summer to early autumn (i.e. February–March), when most native plants have already passed the peak of flowering (Forcone & Kutschker, 2006). During this late flowering period, raspberry flowers are mainly visited by two non-native species, managed honeybees (*Apis mellifera*) and the invasive buff-tailed bumblebee (*Bombus terrestris*; Morales, 2009; Sáez et al., 2014, 2017). Although both species contribute to pollination and increase fruit yield, they can also damage the flowers when visiting them at extremely high frequencies (e.g. >100 visits over a 2-day flower lifespan), which results in reduced fruit quality (Aizen et al., 2014, 2020; Sáez et al., 2014, 2018). Moreover, it has been shown that the invasive *B. terrestris* robs raspberry buds to access nectar, damaging flower structures and decreasing visitation of less damaging honeybees after flower anthesis (Sáez et al., 2014, 2017). However, there is a lack of comparative information on flower visitors and their impacts on fruit quality in early and late flowering periods.

Here we study the phenological overlap between pollinators and crop flowering, focusing on the composition, abundance and richness of pollinators visiting raspberry flowers at two different times during the productive season (i.e. early vs. late), and assess their effects on yield. Because the early flowering of remontant raspberry matches with the flowering peak of the native plant community, while late flowering occurs when the flowering of the native plant community declines (Forcone & Kutschker, 2006; see also Figure 1), we expect the diversity of flower visitors to be higher in the early flowering than in the late flowering period. After proving that pollinator composition varies between the two flowering periods, we investigated whether the turnover in pollinator communities affects flower damage and raspberry yield. Because a higher diversity of pollinators can lead to higher yields (Garibaldi et al., 2013) and an excess of managed or invasive pollinators may result in increased flower damage (Aizen et al., 2014; Sáez et al., 2014), we expect the relative contribution of pollinators to raspberry yield to be higher in the early than in the late flowering period.
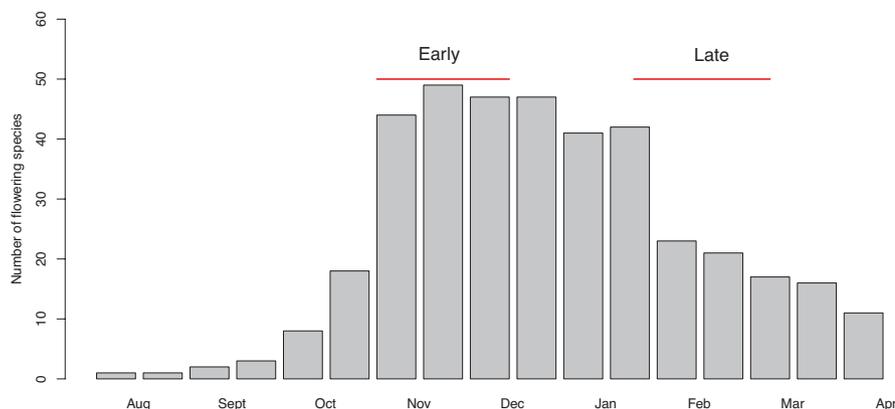
2 | MATERIALS AND METHODS

2.1 | Study area and sites

Fieldwork was conducted during the austral spring (November–December) 2013 and summer (January–March) 2014, in 16 raspberry fields, "Autumn bliss" variety, located in northwestern Patagonia, Argentina. The fields were placed in inter-Andean valleys within the "Andino Norpatagonia Man and Biosphere Reserve" near Lago Puelo National Park and other provincial forest reserves, and thus surrounded by large extensions of natural habitats (Sáez et al., 2014). The cultivated area of the sampled fields ranged from 0.05 to 1.2 ha. All raspberry fields were managed organically, with irrigation and regular fertilization. The minimum distances between sampled fields were always >1 km, a distance that exceeds the mean foraging distance of most social and solitary bees (Osborne et al., 2008; Steffan-Dewenter & Kuhn, 2003; Walther-Hellwig & Frankl, 2000). Thus, each field represents an independent replicate in terms of its foraging bee community.

2.2 | Data collection

In each field, we studied raspberry flower visitors along 20, ~25 m transects: eight to estimate pollinator abundance (i.e. number of pollinators in 200 flowers) and 12 to estimate pollinator richness (i.e. number of pollinator species in 200 flowers) per flowering period (i.e. 20 transects × 2 periods = 40 transects per field in total; Vaissière et al., 2011). Along each transect, we observed a total of 200 focal randomly selected flowers while walking at a regular pace, and recorded the presence and identity of a flower visitor following the methodology proposed by Vaissière et al. (2011). Although these authors do not consider the time spent in each census as a variable to account for, we were careful not to spend more time surveying the 200 flowers on the transects where we observed higher pollinator activity. Pollinators were censused under sunny and moderate or no windy conditions. Half of the transects were monitored in the morning, between 10:00 and 13:00, and the second half in the afternoon, between 14:00 and 17:00. In each field, we surveyed flower

FIGURE 1 Number of native plant species blooming per fortnight along the season in the study region. "Early" and "Late" red horizontal lines indicate the flowering periods of raspberry (*Rubus idaeus*, Autumn bliss variety). Data extracted from de Groot et al. (2023).

visitors over two non-consecutive days within each flowering period (early and late).

We quantified reproductive success in terms of "drupelet set" (i.e. the proportion of ovules that set a drupelet) in naturally (open) pollinated and isolated plants (i.e. plants surrounded with fine mesh precluding pollinator visitation). Drupelet set is a close predictor of fruit weight (Figure S1). In each field, six to eight flowering stems were tagged and randomly assigned to one of two treatments: (a) open (i.e. three to four stems per field/period), or (b) isolated (i.e. three to four stems per field/period). Later, approximately 4 weeks after the survey of flower visitors, we randomly collected fruits from each tagged raspberry stem, totalling 2635 fruits. Fruits were harvested close to maturity (a few days before they easily detached from the receptacle), transported to the laboratory in an electric cooler and stored in a freezer until processing. We used a magnifying glass (20×) to count (1) the number of developed drupelets; (2) the number of undeveloped drupelets (i.e. the presence of a dried stigma without a drupelet); and, in the case of fruits from the open-pollination treatment and (3) the presence/absence of flower damage, measured as the presence of holes in the vestigial sepals (see method in Sáez et al., 2017). Finally, each fruit was weighed using an electronic scale. The proportion of ovules that developed into a drupelet (i.e. drupelet set) is strongly correlated with fresh fruit weight ($r = 0.69$, df = 2193, $t = 44.7$, $p < 0.001$) and can therefore be used as a proxy of crop yield (see Figure S1). Fieldwork and sampling were conducted in agreement with the landowners and no further ethical approval or legal permission was required.

2.3 | Statistical analysis

2.3.1 | Pollinator abundance and richness

We evaluated the effect of crop flowering period (i.e. early vs. late) on (a) total pollinator abundance, (b) abundance of individuals in the different pollinator groups ("*Apis mellifera*", "*Bombus terrestris*", and "native pollinators") and (c) pollinators richness, using a generalized linear mixed-effects model. Because all response variables were counts (i.e. visits or numbers of species), we used a negative binomial distribution and a *log*-link function to account for potential overdispersion in our data. To estimate the effect of the flowering period on the total pollinator abundance (model a), we included the flowering period, a categorical variable with two levels (i.e. early and late), as a fixed effect and transects nested within fields as a random effect, allowing the intercept to vary across fields. For the pollinator type abundance model (b), we included the flowering period and pollinator type, two categorical variables with two (early and late) and three ("*Apis mellifera*", "*Bombus terrestris*" and "native pollinators") levels, respectively, and their interaction as fixed effects, with transects nested within fields as a random effect, allowing the intercept to vary across fields. We assessed these three pollinator groups (i.e. *A. mellifera*, *B. terrestris* and native pollinators) because they represent different pollinator origins and status. While native

pollinators have evolved with the local flora, *A. mellifera* (honeybee) is a non-native species primarily managed for honey production, and *B. terrestris* (buff-tailed bumblebee) is an invasive species that thrives in this region without human assistance (Morales, 2009). Finally, for the species richness (i.e. number of visiting species) model (c), we included crop flowering period (early vs. late) as a fixed effect, with transects nested within fields as a random effect, allowing the intercept to vary across fields.

2.3.2 | Flower damage and drupelet set

First, we assessed the effect of crop flowering period (i.e. early vs. late) on flower damage (proportion of fruits with damaged vestigial sepals), using a generalized linear mixed-effects model. Because the response variable was the presence/absence of damage, we considered a binomial distribution (i.e. 0–1) and a *logit*-link function. The crop flowering period was included in the model as a fixed effect, with plants nested in fields as a random effect, allowing the intercept to vary across fields. Second, we evaluated the effects of pollination treatment (a categorical variable with two levels, open vs. isolated) over the flowering periods on the proportion of fertilized ovules per flower using a generalized linear mixed-effects model. Because the response variable was the proportion of ovules that developed into a drupelet, we used a beta-binomial distribution and a *logit*-link function to account for overdispersion. The pollination treatment and crop flowering period, as well as their interaction, were modelled as fixed effects, with plants nested within fields as a random effect, allowing the intercept to vary across fields. All models were implemented in *R* (R Core Team, 2023) using RStudio (Posit Team, 2023), and the *glmmTMB* function from the *glmmTMB* package (Bolker, 2016). To evaluate pairwise comparisons between the estimated parameters in the different models, we applied the *emmeans* function from the *emmeans* package (Lenth & Love, 2015).

To further examine the effect of the flowering period on the proportion of fertilized ovules, we contrasted quantiles of the density distribution of the number of drupelets produced per ovule using a bootstrap resampling approach. We generated 1000 bootstrap samples of the proportion of ovules fertilized in each flowering period to compute the percentiles (from 5th to 95th) and the distribution of their differences (early–late). From the distribution, we computed the medians and 95% confidence intervals of the difference between the proportion of fertilized ovules in early versus late flowering periods.

3 | RESULTS

In total, we recorded 5378 pollinator visits to raspberry flowers in all 256 transect surveys (i.e. 16 fields × 8 transects per field × two flowering periods). Managed honeybees accounted for nearly 50% of the visits recorded, whereas *B. terrestris* and native pollinators (as a group) accounted for about 25% of the visits each. There was

no evidence that the overall abundance of visiting pollinators in raspberry fields varied between flowering periods (early vs. late, $\beta = -0.02$, SE $= 0.05$, $Z = -0.49$, $p = 0.62$), with an estimated mean ($\pm$SE) total abundance of 19.49 ($\pm$1.11) and 19.88 ($\pm$1.09) visits per 200 flowers during the early and late flowering periods respectively. However, we found strong evidence that pollinator composition differed as the abundance of at least one pollinator type (i.e. either *A. mellifera*, invasive *B. terrestris* or native pollinators) varied between flowering periods (interaction between pollinator type and flowering period, $\chi^2 = 489.96$, df $= 2$, $p < 0.001$). Notably, there was no evidence that the abundance of managed honeybees varied between the two flowering periods ($\beta = 0.06$, SE $= 0.11$, $Z = 0.54$, $p = 0.99$; Figure 2), with an estimated mean ($\pm$SE) abundance of 10.07 ($\pm$1.11) and 9.48 ($\pm$1.11) visits per 200 flowers during the early and late flowering periods respectively. However, the abundance of the invasive *B. terrestris* and native pollinators varied substantially between the two flowering periods but in opposite directions (*B. terrestris*: $\beta = -2.70$, SE $= 0.15$, $Z = -17.16$, $p < 0.001$; native pollinators: $\beta = 1.89$, SE $= 0.13$, $Z = 14.02$, $p < 0.001$; Figure 2). During the early flowering period, *B. terrestris* abundance was estimated at 0.62 ($\pm$1.16) visits per 200 flowers, followed by a 15-fold increase in the late flowering period (9.20 $\pm$ 1.11 visits per 200 flowers; Figure 2). Native pollinators also showed a remarkable change in their abundance, with an estimated value of 8.84 ($\pm$1.11) visits per 200 flowers in the early flowering period, followed by a sixfold decline in the late flowering period (1.33 $\pm$ 1.13 visits per 200 flowers; Figure 2).

The number of pollinator species (richness) that visited raspberry flowers also differed greatly between the two flowering periods ($\beta = -0.56$, SE $= 0.05$, $Z = -9.85$, $p < 0.001$). Pollinator richness was highest during the early flowering period, with an estimated value of 4.43 ($\pm$1.03) species per 200 flowers. This number decreased to an average of 2.5 ($\pm$1.04) species per 200 flowers in the late flowering period (Figure 3a).

Flower damage varied substantially between the two flowering periods. Fruits from the early flowering period showed less damage in their vestigial sepals than fruits from the late flowering period ($\beta = 1.95$, SE $= 0.21$, $Z = 8.90$, $p < 0.001$; Figure 3b). While only 5 ($\pm$0.16) % of the fruits developed during the early flowering period showed signs of damage in the vestigial sepals, this proportion increased sixfold, to an average of 30 ($\pm$5) % during the late flowering period.

The contribution of pollinators to raspberry fruit quality (i.e. the difference between the drupelet set of fruits from open vs. bagged
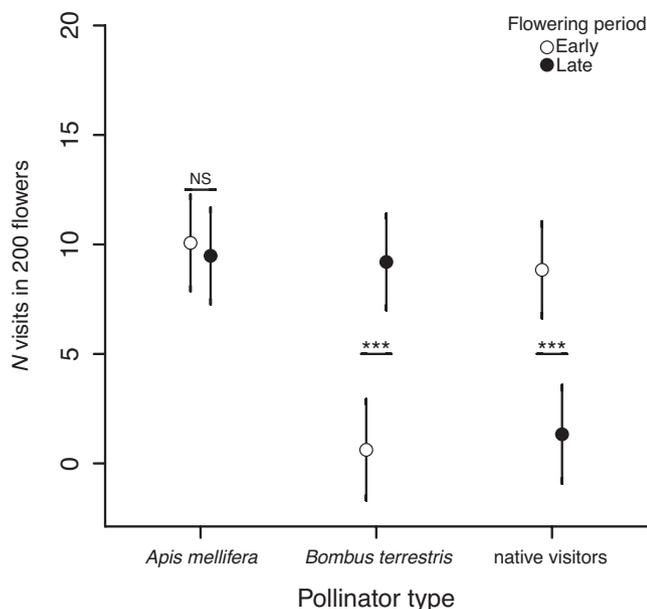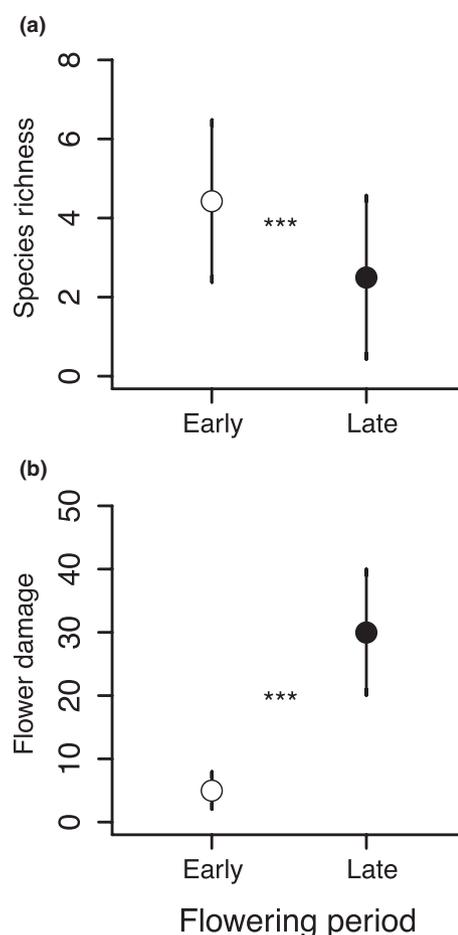
FIGURE 2 Number of visits in 200 raspberry flowers of the different pollinator types (i.e. managed *Apis mellifera*, invader *Bombus terrestris* and native pollinators) during the early and late (white and black respectively) flowering periods. Dots depict estimated mean values and error bars $\pm$ two times SE. ***Statistical differences between flowering periods ($p < 0.001$), while NS indicates no statistical evidence of a difference.

FIGURE 3 Species richness of pollinators (a) and flower damage (b) observed in raspberry fields during early and late blooming periods. Species richness was estimated as the number of species observed on 200 flowers. Flower damage was estimated as the proportion of fruits showing damage in the vestigial sepals. In total, 16 raspberry fields were surveyed over two flowering periods. Dots depict estimated mean values and error bars $\pm$ two times SE. ***Statistical differences between flowering periods ($p < 0.001$).

flowers) varied significantly between the two flowering periods (i.e. the interaction between pollination treatment and flowering period, $\chi^2 = 30.77$, df $= 1$, $p < 0.001$; Figure 4). During the early flowering period, pollinators increased drupelet set by 60.8 (± 1.05) % (mean $\pm$ SE proportional change between open and isolated plants; $\beta = 1.60$, SE $= 0.05$, Z $= 14.74$, $p < 0.001$; Figure 4). In contrast, pollinators increased drupelet set by 30.7 (± 1.02) % during the late flowering period (± 1.02; $\beta = 1.30$, SE $= 0.02$, Z $= 12.79$, $p < 0.001$; Figure 4). The observed change in pollinators contribution between flowering periods may be attributed, partially, to an increase in drupelet set in the isolation treatment during the late flowering, from a drupelet set of 0.42 (± 0.02) in the early period to 0.52 (± 0.02) during the late period (Figure 4; Table 1). Although open pollination resulted in similar average pollination rates in the two periods (i.e. ca. 0.68,

see Figure 4; Table 1), analysis of frequency distributions (quantiles) revealed significant differences in the distribution of drupelet set between the early and late periods, particularly for the quantile 0.9 ($\Delta_{\text{early-late}} = 0.04$, $p < 0.001$), 0.75 ($\Delta_{\text{early-late}} = 0.04$, $p < 0.001$), 0.5 ($\Delta_{\text{early-late}} = 0.04$, $p = 0.01$) and 0.25 ($\Delta_{\text{early-late}} = 0.09$, $p = 0.003$; Table S1). Raspberry flowers produced in the early period are more likely to have a higher proportion of ovules fertilized than those produced in the late period (Figure 5; Table S1).

4 | DISCUSSION

The synchrony between flowering time and the availability of diverse pollinator communities is a crucial trait for crop pollination, and thus for more than 75% of global crops (Klein et al., 2007). Despite its importance, the evaluation of temporal matches or mismatches between crop flowering and the density and composition of the pollinator community has been poorly studied (but see Sritongchuay et al., 2021). This is most likely due to the methodological challenges associated with assessing temporal changes in plant–pollinator interactions in crops that generally bloom for short periods. We overcame these challenges by taking advantage

TABLE 1 Post-hoc estimations from the drupelet set model using *emmeans* function to perform pairwise comparisons between estimated parameters under different treatments (i.e. flowering period × pollination treatment). Different letters in the "Group" column indicate statistical differences between them ($p < 0.05$).

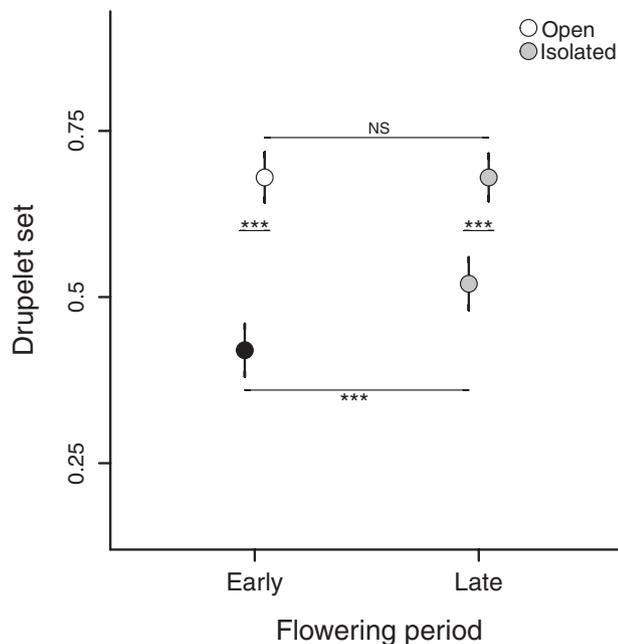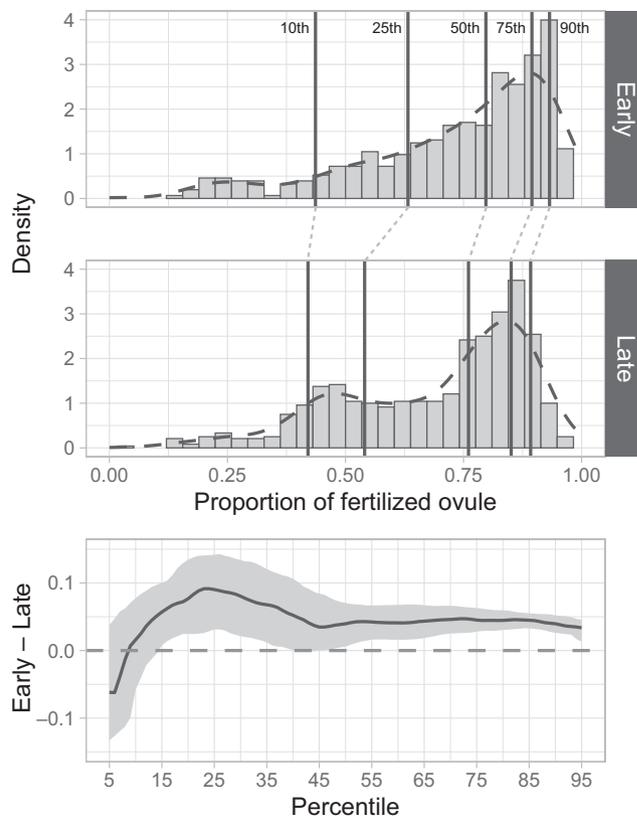| Flowering period	Pollination treatment	Estimated drupelet set	SE	Group
Early	Open	0.68	0.01	a
Late	Open	0.67	0.01	a
Early	Isolated	0.42	0.02	c
Late	Isolated	0.52	0.02	b

FIGURE 4 Drupelet set (proportion of ovules that developed into a drupelet) counted on fruits harvested during the early and late flowering periods from open (white) and isolated (grey—excluded from pollinators) plants. Dots depict estimated mean values and error bars ± two times SE. ***Statistical differences between flowering periods ($p < 0.001$), while NS indicates no statistical evidence of a difference.

FIGURE 5 Differences in the proportion of ovules fertilized (drupelet/ovule) in the early versus late flowering period of the raspberry variety Autumn bliss. Differences between early and late flowering period are represented per percentile (between the 5th and 95th). Median and 95% confidence interval of the difference was computed from 1000 bootstrap samples.

of the remontant Autumn bliss raspberry, a variety that blooms twice a year. We found evidence that the composition of flower visitors varies over time and that this variation affects crop yield. These results show how phenological overlap between native pollinator foraging periods and crop flowering can result in better pollination services.

During the early flowering period of raspberry, which matches with the flowering peak of the native flora, the abundance and richness of native pollinators were both notably higher than during the late flowering period, when flower resources in the native flora become scarce (see Forcone & Kutschker, 2006; Figures 1–3). This is most likely the result of the strong seasonality that characterizes most agricultural and natural ecosystems (Ellis et al., 2017; Hirao et al., 2006). Importantly, the temporal changes in the abundance and richness of native pollinators reported here were not confounded with a displacement caused by the invasive *B. terrestris*, as indicated by the absence of a negative correlation between these two pollinator groups (Appendix S1; Figure S2). Using a different approach, Sritongchuay et al. (2021) also showed that artificially induced changes in flowering phenology in longan fruit trees (*Dimocarpus longan*) resulted in reduced yield due to overlapping with a period of lower activity of native pollinators. Together, these results highlight the importance of the phenological overlap between crop flowering and local pollinator fauna. Not surprisingly, the temporal alignment between crop flowering and pollinator activity is essential for effective interactions and high-quality crop pollination (Peralta et al., 2020; Sritongchuay et al., 2021).

Such temporal variation was also observed in the abundance of the invasive bumblebee, whose temporal pattern contrasted with that of native species. The number of *B. terrestris* was low in spring and increased later in the summer. The seasonal pattern observed in *B. terrestris* visitation can be explained by the species' life history, particularly associated with the seasonality in its colony development. In spring (early raspberry flowering period), foundress queens mainly search for suitable nesting sites, lay eggs and start the colony development (Mola et al., 2021). Indeed, very few *B. terrestris* visits were recorded during the early flowering period, and most visiting bumblebees were queens. This contrasts with the flower visits recorded later in the summer, when *B. terrestris* colonies are fully developed and the number of workers scouting the environment and foraging on flowers reaches its maximum (Morales et al., 2013). This remarkable change in the abundance of the invasive bumblebee also affects the quality of pollination services observed in raspberry crops during the two flowering periods. During the late flowering period, when managed honeybees and invasive bumblebees dominated the pollinator community visiting raspberry flowers, interaction costs measured as flower damage increased significantly (Aizen et al., 2014, 2020; Sáez et al., 2014).

In contrast, the number of managed honeybees observed on raspberry flowers did not change between the two flowering periods. Most, if not all, beekeepers in northwest Patagonia are sedentary (i.e. hives stay in their apiaries year-round) and almost evenly distributed in productive lands at valley bottoms. The Interamerican Institute for Cooperation on Agriculture (IICA) reported in 2013 the existence of 2500 hives in the study area, most of them owned by small-scale producers (5–10 hives; Baquero et al., 2013). Thus, the number and location of hives in each landscape remain relatively constant over the years and between flowering periods. Beyond the number of hives, honeybee foraging is sustained throughout the warm season in temperate regions, with high hive populations between November and February, after which populations start declining due to a shortage in floral resources and lower temperatures at the end of the Patagonian summer. However, studies on the carrying capacity at local and landscape scales are necessary to avoid overloading the environment with an alien pollinator that could eventually compete with native pollinators.

The contribution of pollinators to crop yield varied greatly between the two flowering periods. During the early flowering period, pollinators increased raspberry yield (measured as the proportion of ovules that developed into a drupelet in open and isolated plants) by ca. 60%, while this contribution declined to ca. 30% in the late flowering period. At least four, not mutually exclusive, hypotheses can be postulated to explain the difference observed in the relative contribution of pollinators between the two flowering periods: (1) variation in species composition of the pollinator community, (2) change in the degree of autonomous self-pollination, (3) change in resource availability and (4) different rates of flower damage over the two periods.

First, we observed that the pollinator community was much more diverse during the early flowering period than during the late flowering, which was almost exclusively dominated by managed honeybees and the invasive *B. terrestris*. Several studies have shown the positive effect of increased pollinator richness on fruit and seed production, often referring to the increase in functional diversity and complementary resulting from more diverse pollinator communities (see Woodcock et al., 2019, and references therein). Second, a higher rate of autonomous self-pollination in the late flowering period could lead to a reduced contribution of pollinators to raspberry flower fertilization (Figure 4; Table 1; Strelin & Aizen, 2018). Third, because of a plant's modular structure and partial physiological integration, the drupelet set of at least some autonomously self-pollinated flowers could be more limited by resources than by pollination, even in the absence of pollinator visitation. Because the new stems (late-flowering) are more resourceful than the old stems (early flowering), the basal drupelet set of isolated flowers might be expected to be higher during the late than the early flowering period (Figure 4; Strelin & Aizen, 2018). Similarly, under adequate pollination, the drupelet set of open flowers should be close to 100% during late flowering since resources would not limit production (Strelin & Aizen, 2018). However, our results show that the frequency of high-quality fruits in the late flowering period was lower than in the early flowering period. This difference could be explained by the increase in flower damage observed in the late flowering period (hypothesis 4). We found that the higher abundance of *B. terrestris* during the late flowering period coincided with a higher proportion of damaged flowers. Previous studies have shown that flower and bud damage,

associated with an overabundance of a pollinator, decreases raspberry fruit quality (Aizen et al., 2014; Sáez et al., 2014). Although further work is needed to assess the relative contribution of each of these factors, previous studies conducted in this crop system have shown that in the absence of either pollination or resource limitation, the drupelet set can be maximized and only be limited by the number of ovules produced per flower (Strelin & Aizen, 2018). This should result in fruits of maximum quality. However, the frequency of fruits with high drupelet set (i.e. close to 100%) was lower in the late than in the early flowering period. In fact, there was a notable proportion of flowers having less than 50% of their ovules fertilized in the late flowering period (see Figure 5). This temporal contrast resembles differences found by Sáez et al. (2014) between fields with low and high flower damage (Figure S3). Therefore, the fact that a high proportion of fruits did not reach high-quality standards during the late flowering period is most likely due to increasing flower damage associated with the increasing dominance of *B. terrestris* (Sáez et al., 2014, 2017).

5 | CONCLUSIONS

Global agriculture is becoming increasingly pollinator dependent (Aizen et al., 2008, 2019). In parallel, there is bulk evidence showing that diverse pollinator communities are required to properly pollinate and maximize yields in pollinator-dependent crops (Garibaldi et al., 2013, 2016; Woodcock et al., 2019), and that single-species management (i.e. honeybees) does not entirely solve yield losses associated with pollination limitation in many crops (Sáez et al., 2022). However, plant–pollinator interactions are temporally structured (Peralta et al., 2020) and phenological overlaps between local pollinators and crop flowering are essential aspects to consider when planning and managing cropping systems, as the foraging period of local pollinators can significantly contribute to maximizing the benefits of pollination services provided by native species. On the land-manager side, maintaining or restoring natural and semi-natural habitats in agricultural landscapes with native plant communities with extended flowering periods and complementary phenology can provide more reliable floral resources and support diverse pollinator assemblages for longer periods (Peters et al., 2013; Timberlake et al., 2019). On the grower and crop breeding side, selection flowering time could be targeted to match the periods of high diversity of local pollinators. This will help decrease the dependence on external inputs (e.g. managed pollinators) for pollination services and benefit growers while preserving biodiversity.

AUTHOR CONTRIBUTIONS

Agustín Sáez, Marcelo A. Aizen and Lucas A. Garibaldi conceived the ideas; Lucas A. Garibaldi designed the methodology; Agustín Sáez, Grecia de Groot and Carolina L. Morales collected the data; Agustín Sáez, Marcelo A. Aizen and Reto Schmucki analysed the data. Agustín Sáez, Marcelo A. Aizen, Anna Traveset, Carolina L. Morales, Reto Schmucki and Lucas A. Garibaldi interpreted and discussed the results; Agustín Sáez, Marcelo A. Aizen and Reto Schmucki led the writing of the first draft of the manuscript. All authors contributed critically to the final draft and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT
The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT
Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.1c59zw42f (Sáez 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.

Figure S1. Relation between drupelet set and fruit weight.

Figure S2. Relation between the abundance of *Bombus terrestris* and the native pollinator community.

Figure S3. Histograms of drupelet set for fruits with low and high damage.

Table S1. Differences in the proportion of fertilized ovules in raspberries flower pollinated early (spring) and late (autumn) in the flowering season.

Appendix S1. Effects of the invader *Bombus terrestris* on native pollinators and possible confounding effects.