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Is Nocturnal Pollination Important for Crop Production? Experimental Evidence From Small Fruit Crops

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ABSTRACT

Insect-mediated pollination is essential for crop production but is mainly studied considering diurnal pollinators only. Here, we use pollinator exclusion techniques to prevent either diurnal or nocturnal insect visits in small fruit crops: raspberry (*Rubus idaeus*), over 1 year, and red currant (*Ribes rubrum*) and black currant (*Ribes nigrum*), over 2 years, in sites within mixed landscapes of western and northern France. The contribution of day- and night-active pollinators was measured from 850 flowers total from 36 plants across all species and included the following pollination components: fruit set, fruit weight, fruit volume and seed set. We find that nocturnal pollination improves seed set of all three crops, as well as fruit volume of red currant, compared to exclusion of all insect visits. This confirms the existence of nocturnal pollination services for these crops. We found no direct evidence of a nocturnal pollination service for fruit set of the three crops. However, we found that contributions from the combination of diurnal and nocturnal pollinators enhance fruit set in red currant and black currant. We found no effects of pollination treatment on fruit weight of any crop. These results suggest that nocturnal pollination plays a role in the production of small fruit crops, and call for inclusive pollinator-friendly schemes including night-active pollinators in order to support pollination services and crop production.

1 | Introduction

Animal pollination is essential for the reproduction of 87.5% of all flowering plants (Ollerton et al. 2011), and the production of over half of the leading crops worldwide (Klein et al. 2007). The crop pollination service is valued at 195–387 billion US dollars annually (Porto et al. 2020). In agriculture, animal pollination has implications for food security, since many animal-pollinated crops contain nutrients required for a healthy human diet (Garibaldi et al. 2022; Smith et al. 2022; Smith et al. 2015). In addition, pollination has value in areas such as medicine, the production of biofuels, or even the reproduction of aesthetically important plants (Garibaldi et al. 2022; Potts et al. 2016).

Beyond the Western honey bee *Apis mellifera*, known as an economically important pollinator in agriculture (Reilly et al. 2024; Sagwe et al. 2021), wild insect pollinators provide significant and essential contributions to crop pollination (Garibaldi et al. 2013; Rader et al. 2016; Rader et al. 2020; Requier et al. 2023), as do some non-insect pollinators in the tropics, such as birds and bats (Ratto et al. 2018; Requier et al. 2023). The evidence of a decline in insect pollinators (Biesmeijer et al. 2006; Dicks et al. 2021; Koh et al. 2016) raises alarm for the resilience of their supporting pollination services to pollinator-dependent crops (Potts et al. 2016). Indeed, less diverse biological communities are often thought to provide ecosystem services that are less resilient to disturbance

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over space or time (Cariveau et al. 2013; Martin et al. 2019). Crop pollination is therefore commonly cited as an example of an endangered ecosystem service, with evidence of pollination deficits, for example in apple (*Malus domestica*) (Rosaceae) (Garratt et al. 2021; Olhnuud et al. 2022) and highbush blueberry (*Vaccinium corymbosum*) (Ericaceae) (Button and Elle 2014). These pollination deficits are particularly pronounced in intensive agricultural landscapes (Bartomeus et al. 2014), a main driver of global environmental changes that negatively impact pollinator diversity (Dicks et al. 2021). Pollinator-friendly agricultural practices are thus recommended to protect pollinator communities (Garibaldi et al. 2017; Requier and Leonhardt 2020), such as restoring semi-natural habitats (Kremen and M'Gonigle 2015), planting wildflower borders (Grab et al. 2018), providing nesting habitats (Potts et al. 2005), and reducing intensive farming practices (Hardman et al. 2016).

However, most of our knowledge about pollination and pollinators focuses on diurnal activity, neglecting the contribution of nocturnal pollinators to crop production (Buxton et al. 2022; Requier et al. 2023). Night-active pollinators include vertebrates such as bats (under tropical climates) as well as invertebrates such as moths, beetles and some bee species (Anderson et al. 2023; Buxton et al. 2022; Ellis et al. 2023; Hahn and Brühl 2016; Knop et al. 2018; Lu et al. 2021; Macgregor and Scott-Brown 2020; Nicholls et al. 2023; Walton et al. 2020). Since they are relatively understudied, nocturnal pollinators could face specific threats such as Artificial Light At Night (Macgregor et al. 2015) or night-time pesticide applications (Decourtye et al. 2016). However, their contribution to crop pollination is increasingly recognised, with nocturnal pollinators observed visiting flowers of numerous tropical and temperate crops (Requier et al. 2023; Torretta et al. 2009), with recent studies revealing their contributions to the pollination of avocado (*Persea americana*) (Buxton et al. 2022), apple (*Malus domestica*) (Rosaceae) (Robertson et al. 2021), strawberry (*Fragaria x ananassa*) (Rosaceae) (Fijen et al. 2023) and buckwheat (*Fagopyrum esculentum*) (Polygonaceae) (Nagano and Miyashita 2024) crops.

The objective of this study was to explore the contribution of nocturnal pollinators across three small fruit crops: raspberry (*Rubus idaeus*) (Rosaceae), red currant (*Ribes rubrum*) (Grossulariaceae) and black currant (*Ribes nigrum*) (Grossulariaceae). Results that demonstrate benefits from nocturnal pollination can be leveraged to guide more inclusive pollinator enhancement schemes. Specifically, we ask what is the contribution of nocturnal and diurnal pollination services of these small fruit crops. To address this, several yield components including fruit set, fruit weight, fruit volume and seed set were measured on these three crops when exposed to different pollination scenarios with separate consideration of diurnal and nocturnal pollinators, as well as their combined effect. These crops are known to benefit from animal pollination (Klein et al. 2007), but the contribution of nocturnal pollination is yet to be assessed. We hypothesise that diurnal-only pollination, nocturnal-only pollination, and both combined will positively affect all yield components measured. Indeed, having functionally diverse pollinator communities improves plant reproductive success and crop yield in several studies

(Albrecht et al. 2012; Fründ et al. 2013), thus the combination of diurnal and nocturnal pollinators should enhance yield components more than the diurnal-only or nocturnal-only treatments.

2 | Materials and Methods

2.1 | Study Sites

The experiment was carried out in 2020 and 2024 on two study sites located in France. The first study site was located in the protected area *Parc Naturel Régional Périgord-Limousin* in western France (45°34'16.2"N 0°55'05.5"E), which hosted the 2020 experiment (from March to July). The land cover was composed of a mixed landscape with 38% grassland, 38% forest, 23% agricultural and 1% urban habitats with bodies of water in a 1.5 km radius (Itsap 2023). This site contained an apiary of five hives, located approximately 100 m from the crops. The second study site was located in a suburban area approximately 20 km south west of Paris (48°42'42.4"N, 2°03'47.7"E), which hosted the 2024 experiment (a repetition of the 2020 experiment, also from March to July). The land cover was composed of 41% discontinuous urban, 35% forest and 24% agricultural habitats in a 1.5 km radius (Itsap 2023). The nearest apiary (approx. 30 hives) was more than 1 km away from this site.

2.2 | Studied Crops

The three study crops were raspberry (*Rubus idaeus*, cultivar Zeva), red currant (*Ribes rubrum*, cultivar Versailles Rouge) and black currant (*Ribes nigrum*, cultivar Black Down). Yields are known to decrease in the absence of pollinators for raspberry (Andrikopoulos and Cane 2018; Chen et al. 2021), with higher pollinator dependency for raspberry than red currant (Klein et al. 2007). Similarly, black currant yields benefit from animal pollination (Koltowski et al. 1999). The three crops have radially symmetrical flowers, which are cup-shaped. Raspberry petals are white, while red currant petals are pinkish. Black currant flowers are smaller than those of the other crops and have white to red petals (WFO 2025). Considering these floral morphologies, these flowers can be considered as functional and ecological generalists, that is, they can be visited by a wide array of insects which all contribute to pollination (Ollerton et al. 2007). Moreover, all three crops have flowers that remain open for at least 48 h (Bekey 1985; Kampuss and Pedersen 2003; Zurawicz et al. 1999), that is, including day and night, making them potential candidates for nocturnal pollination. All three crops were used in 2020, whereas only black currant and red currant were used in 2024, since there were too few flowers available on raspberry to run the experiment on this crop in 2024. The same plant cultivars were used at both sites over the 2-year period (2020 and 2024), with cuttings taken from the same original plant. The two study sites, both within private gardens, were similar in terms of spatial arrangement of crops (plants were present within 100 m² area) and cover intensity, with about 20 raspberry plants, 25 red currant plants and 40 black currant plants. Plants of all species were approximately 5 years old on the site used in 2020 and 4 years old on the site used in 2024. A subset of 36 plants (12

plants in 2020 and 24 plants in 2024) was randomly selected for the pollination treatment experiments.

2.3 | Diurnal Pollinator Observations

Diurnal pollinator observation sessions were performed between the 3rd of March 2020 and the 30th of April 2020. Raspberry and black currant flowers were observed at 17 occasions, and red currant flowers were observed 18 times. A total of 147 raspberry flowers (average of 8.65 flowers per session) were observed, 552 red currant flowers (average of 30.67 flowers per session) and 756 black currant flowers (average of 44.47 flowers per session). Each observation session lasted 5 min. Pollinators observed were sorted into the following nine categories: honey bee (*Apis mellifera*), bumble bee (*Bombus* sp.), wild bee, hoverfly (Syrphidae), other fly (Diptera), wasp (Vespidae), ant (Formicidae), beetle (Coleoptera) and spider (Aranea).

2.4 | Pollination Treatments

We randomly selected four inflorescences (i.e., racemes in red currant and black currant) on the selected plants to carry out pollination treatments. Flowers within inflorescences were tracked individually. Four pollination treatments were then allocated to these flower groups, with one treatment per flower group, as follows: flowers excluded from pollinator visits (Closed), flowers open to pollinator visits only during the day (Day) and only during the night (Night), and flowers open to pollinator visits during both day and night (Day+Night). Due to constraints related to plant morphology, as is typically done in the literature (e.g., Anderson et al. 2023; Latet et al. 1999; Ryan et al. 2023), it was not possible to apply different treatments within the same inflorescence. All treatments were replicated on different plants. Pollinator exclusion was achieved by bagging flowers with mesh netting, preventing any insect visits (Alt'Droso Maraichage, 0.8×0.8mm mesh). Flowers allocated to the Night treatment were unbagged at sunset (7:00PM) and exposed to pollinators for 11 h and 30 min per day. Those allocated to the Day treatment were unbagged at sunrise (7:30AM) and were exposed to pollinators for 12 h and 30 min per day. Flowers allocated to the Day+Night treatment were exposed continuously to pollinators. Thus we measure pollination service provided by all pollinators (Closed vs. Day+Night), diurnal pollinators only (Closed vs. Day) and nocturnal pollinators only (Closed vs. Night) (Garratt et al. 2021).

In total, 850 flowers were used as part of the experiment (329 in 2020 and 521 in 2024), with 54 raspberry flowers (only in 2020), 421 red currant flowers (134 in 2020 and 287 in 2024) and 375 black currant flowers (141 in 2020 and 234 in 2024). The inflorescences allocated to each pollination treatment were composed of 6.75 ± 1.98 flowers (mean $\pm$ sd) for raspberry, 11.69 ± 6.23 flowers for red currant and 10.42 ± 5.14 flowers for black currant.

2.5 | Fruit Measurements

Once flowering was over and fruits began to form, we measured fruit set of all three crops at the level of the inflorescence, recording for each inflorescence the number of flowers which

successfully or unsuccessfully formed a fruit. Fruits from all three crops were harvested over June and July in both 2020 and 2024. We measured fruit weight, fruit volume, and seed set on all fruits that were successfully formed. We measured fruit weight using scales (Brifit, Digital Kitchen Scale, accuracy 0.01 g, capacity 500 g in 2020 and Sartorius ED822-CW Extend Precision Balance, accuracy 0.01 g, capacity 820 g in 2024). We estimated fruit volume using two measures of fruit size: maximum height and width (Mitutoyo, Digimatic Calliper, accuracy 0.01 mm, capacity 150 mm, accuracy 0.01 mm, capacity 150 mm in 2024). Assuming the shape of a raspberry is half of an ellipsoid, we used the following formula to calculate fruit volume:

$$\text{Fruit volume (raspberry)} = \frac{1}{2} \left(\frac{4}{3} \pi \times \text{height} \times \left(\frac{1}{2} \text{width} \right)^2 \right)$$

Red currant and black currant volumes were computed assuming fruits are shaped like spheres:

$$\text{Fruit volume (red currant, black currant)} = \frac{4}{3} \pi \times \left(\frac{1}{2} \text{height} \right)^3$$

In addition, we measured seed set by separating the flesh from the seeds and counting the number of seeds produced by each fruit.

These metrics are not linked to commercial standards for these crops (Groupe de travail des normes de qualité des produits agricoles 2021) but were chosen since they are known to respond to pollination treatments for blueberry (Button and Elle 2014; Ramírez-Mejía et al. 2023) and raspberry (Hall et al. 2020).

2.6 | Statistical Analysis

The statistical analysis was performed in R 4.3.2 (R Core Team 2025). We performed an a posteriori statistical power analysis to assess the sample size required to detect effects of nocturnal pollination (if it occurs), using paired *t* test power calculations (the *power.t.test* function of the *stats* package in R, R Core Team 2025), and based on data from a study which revealed the benefits of nocturnal pollination on strawberry weight (Fijen et al. 2023). We calculated the difference in mean and standard deviation of fruit weight between strawberries allocated to the nocturnal pollination treatment and those excluded from all pollinator visits, considering a threshold of 0.05 for the significance level (Type I error probability), and a power of the test of 0.95 (Type II error probability).

We tested the effects of pollination treatments on fruit set using a generalised linear model (GLM) with binomial error structure. We used the inflorescence as statistical unit, thus analysing the proportion of successes and failures within each inflorescence. This model predicts the probability of fruit set success for each treatment. After checking for normality using a Shapiro–Wilk test, we used linear models (LM) to test the effects of pollination treatments on fruit weight and fruit volume, using single fruit as the statistical unit, and applied square root transformations for the cases in which normality was not verified. We used a square root transformation for fruit weight and fruit volume of red currant and

black currant in order for the data to follow a normal distribution. Moreover, we used a GLM with Poisson error structure to test for effects of pollination treatment on seed set, also using single fruit as statistical unit. We pooled together the data from both years, and added year as an explanatory variable in all the models for red current and black currant. These models were generated using the *stats* R-package (R Core Team 2025). We considered a threshold of 5% for significance. We used Type II Anova from the *car* R-package (Fox and Weisberg 2019) to test significance of model parameters, using Chi² Wald tests for GLMs and F tests for LMs. Means were compared when the parameter was significant using Tuckey post hoc tests, (*multcomp* R-package (Hothorn et al. 2008)). We used the *dplyr* R-package in our data management (Wickham et al. 2023), the *ggeffects* R-package (Lüdtke 2018) for generating predictions from models, and *base* and *ggplot2* R-packages to generate graphs (Wickham 2016).

3 | Results

3.1 | Diurnal Pollinator Observations

We observed 109 diurnal visits on raspberry flowers in total (frequency of 0.39 visits per flower per minute), with ants as the main diurnal visitors (67 visits), followed by bumble bees (25 visits), honey bees (15 visits), hoverflies (1 visit) and spiders (1 visit). We observed 7 visits to red currant flowers (frequency of 0.01 visits per flower per minute), all flies. We observed 23 visits to black currant flowers (frequency of 0.02 visits per flower per minute). These were predominantly by flies (10 visits), followed

by ants (6 visits), bumble bees (5 visits), wasps (4 visits), beetles (2 visits) and wild bees (1 visit).

3.2 | Fruit Set and Fruit Development

We found that a minimum of 36.4 ± 6.2 fruits (mean ± sd) is needed to observe a nocturnal pollination effect, if it exists, based on the a posteriori statistical power analysis (Figure S1). Our sample sizes of successfully formed fruits (45 raspberry fruits, 151 red currant fruits and 63 black currant fruits) had 97.9%, 99.7% and 99.9% chances to detect nocturnal pollination effects, respectively (Figure S1).

For raspberry, fruit set per inflorescence was an average proportion of 0.81 ± 0.27. There was no effect of treatment on the probability of fruit set for this crop (Figure 1a, Table 1). For red currant, fruit set per inflorescence was an average proportion of 0.36 ± 0.21 flowers. Pollination treatment and year had significant effects on the probability of fruit set (Table 2). Fruit set probability was higher in both the Day and Day + Night treatments compared to the Closed treatment (*p* = 0.020 and *p* < 0.001 respectively, Figure 1b, Table S2). There were no significant differences between the other treatments (Figure 1b, Table S2). Fruit set probability was significantly higher in 2020 than in 2024 (*p* = 0.013, Table 2). For black currant, fruit set per inflorescence was an average proportion of 0.14 ± 0.18 flowers. Pollination treatment had a significant effect on fruit set probability for this crop, whereas year had no effect (Table 3). Fruit set probability was significantly higher in the Day + Night treatment compared

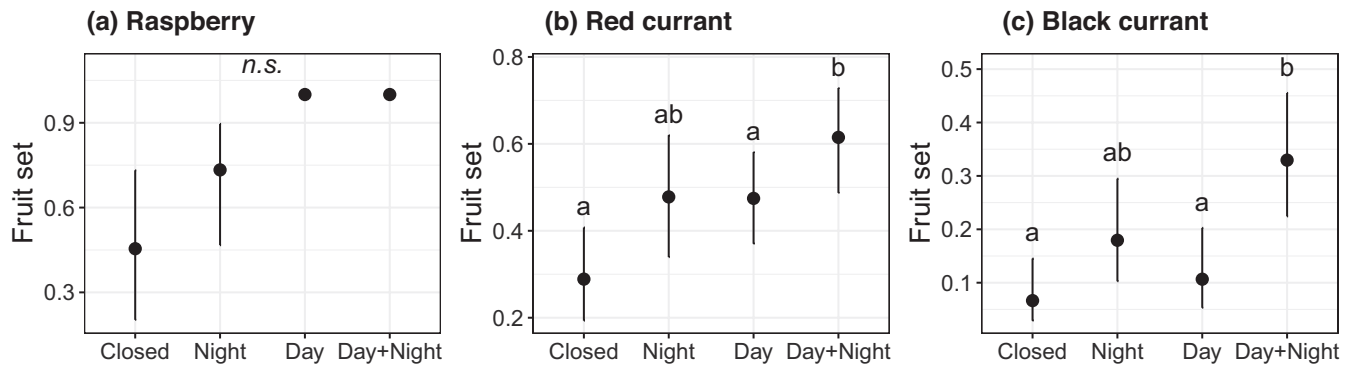


FIGURE 1 | Comparing fruit set between Closed, Night, Day and Day + Night pollination treatments in (a) raspberry, (b) red currant and (c) black currant. Dots represent the predicted fruit set per pollination treatments, with thick lines indicating the 95% CI (based on GLM predictions). Different small letters indicate significant differences with a risk of 5%, and *n.s.* represents non-significant difference.

TABLE 1 | Summary of Generalised Linear Models (GLMs) and Linear Models (LMs) evaluating the impact of pollination treatment on raspberry fruit set, seed set, fruit weight and fruit volume. Significant effects (*p* < 0.05) are indicated in bold. Statistics were computed from Chi-Squared Wald tests for GLMs and F tests for LMs (type II Anova, from the “car” package in R).

GLMs			LMs			
Parameter	χ ²	<i>p</i> value	Parameter	Sum of squares	F-value	<i>p</i> value
<i>Fruit set</i>			<i>Fruit weight</i>			
Treatment	2.015	0.569	Treatment	2.055	1.523	0.223
<i>Seed set</i>			<i>Fruit volume</i>			
Treatment	77.889	< 0.001	Treatment	3.033	1.236	0.310

to the Closed treatment ($p < 0.001$), and compared to the Day treatment ($p = 0.003$) (Figure 1c, Table S3). Fruit set probability was marginally higher in the Night treatment compared to the Closed treatment ($p = 0.082$, Table S3).

3.3 | Fruit Weight and Volume

For raspberry, there was no effect of treatment on fruit volume or fruit weight (Table 1, Figure 2a, Figure 3a). For red

currant, we found a significant effect of treatment on fruit volume (Table 2, Figure 3b). This metric was greater in both the Night treatment and the Day treatment compared to the Closed treatment ($p = 0.037$ and $p = 0.039$ respectively, Table S2, Figure 3b). However, there was no effect of treatment on red currant fruit weight (Table 2, Figure 2b). We found that fruit volume and fruit weight were greater in 2020 than in 2024 ($p < 0.001$ and $p < 0.001$ for fruit volume and fruit weight respectively, Table 2). For black currant, we found no effect of treatment on fruit volume or fruit weight (Table 3,

TABLE 2 | Summary of Generalised Linear Models (GLMs) and Linear Models (LMs) evaluating the impact of pollination treatment and experimental year on red currant fruit set, seed set, fruit weight and fruit volume. Significant effects ($p < 0.05$) are indicated in bold. Statistics were computed from Chi-Squared Wald tests for GLMs and F tests for LMs (Anova function from “car” package in R).

GLMs			LMs			
Parameter	χ^2	p value	Parameter	Sum of squares	F-value	p value
<i>Fruit set</i>			<i>Fruit weight (square root transformation)</i>			
Treatment	20.239	< 0.001	Treatment	0.123	1.608	0.192
Year	6.155	0.013	Year	0.854	33.617	< 0.001
<i>Seed set</i>			<i>Fruit volume (square root transformation)</i>			
Treatment	22.043	< 0.001	Treatment	0.153	2.770	0.045
Year	18.978	< 0.001	Year	0.409	22.225	< 0.001

TABLE 3 | Summary of Generalised Linear Models (GLMs) and Linear Models (LMs) evaluating the impact of pollination treatment and experimental year on black currant fruit set, seed set, fruit weight and fruit volume. Significant effects ($p < 0.05$) are indicated in bold. Statistics were computed from Chi-Squared Wald tests for GLMs and F tests for LMs (Anova function from “car” package in R).

GLMs			LMs			
Parameter	χ^2	p value	Parameter	Sum of squares	F-value	p value
<i>Fruit set</i>			<i>Fruit weight (square root transformation)</i>			
Treatment	23.410	< 0.001	Treatment	0.131	1.967	0.130
Year	0.014	0.908	Year	0.873	39.454	< 0.001
<i>Seed set</i>			<i>Fruit volume (square root transformation)</i>			
Treatment	19.564	< 0.001	Treatment	0.060	0.954	0.421
Year	0	0.995	Year	0.797	37.826	< 0.001

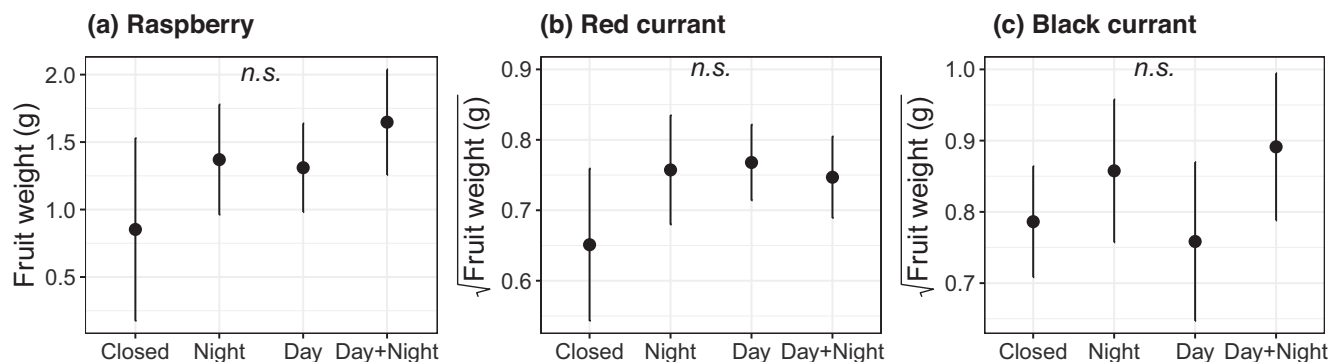


FIGURE 2 | Comparing fruit weight (in g) between Closed, Night, Day and Day+Night pollination treatments in (a) raspberry, (b) red currant and (c) black currant. Dots represent the predicted fruit set per pollination treatments, with thick lines indicating the 95% CI (based on GLM predictions). n.s. represents non-significant difference.

Figure 2c, Figure 3c). However, we found that these two metrics were greater in 2020 than in 2024 for this crop ($p < 0.001$ and $p < 0.001$ respectively, Table 3).

3.4 | Seed Set

For raspberry, pollination treatment had a significant effect on seed set (Table 1), with seed set being significantly lower in the Closed treatment compared to the Night treatment ($p < 0.001$), the Day treatment ($p < 0.001$) and the Day + Night treatment ($p < 0.001$) (Figure 4a, Table S1). Seed set was also lower in the Night treatment compared to the Day treatment for this crop ($p < 0.001$, Figure 4a, Table S1). For red currant, both pollination treatment and year had a significant effect on seed set (Table 2). Seed set was lower in the Closed treatment compared to the Night treatment ($p = 0.004$), the Day treatment ($p < 0.001$) and the Day + Night treatment ($p < 0.001$) (Figure 4b, Table S2). Seed set was significantly lower in 2024 compared to 2020 ($p < 0.001$, Table S2). For black currant, pollination treatment had a significant effect on seed set, but there was no effect of year (Table 3). Seed set was lower in the Closed treatment compared to the Night treatment ($p < 0.001$) and compared to the Day + Night treatment ($p = 0.017$) (Figure 4c, Table S3). It was also lower in the Day treatment compared to the Night treatment ($p = 0.007$) (Figure 4c, Table S3).

4 | Discussion

The results reported here suggest that nocturnal pollinators provide a contribution to pollination in small fruit crops, in particular with regard to seed set of all three crops, as well as fruit volume of red currants, which were improved by exposure to nocturnal pollinators, compared to the absence of any pollinator visits. This confirms a nocturnal pollination service for these crops, in the context of this study. These results follow findings from studies carried out on other crops such as avocado (Buxton et al. 2022), kiwi (*Actinidia chinensis*) (Actidiaceae) (Broussard et al. 2022), apple (Robertson et al. 2021), strawberry (Fijen et al. 2023) lowbush blueberry (Cutler et al. 2012) and buckwheat (Nagano and Miyashita 2024), leading to increasing evidence of nocturnal contributions to crop pollination. Since temporal niche complementarity enhances pollination across the day (Pisanty et al. 2016), it is not surprising that this extends to pollinators active at night. Exposure to nocturnal pollinators increases both the abundance and diversity of flower visitors, since species active at night tend to differ from those active during the day (Anderson et al. 2023; Broussard et al. 2022; Knop et al. 2018). Moreover, nocturnal pollinators can be efficient pollinators, in particular with regard to conspecific pollen transfer (Anderson et al. 2023; Razanajatovo et al. 2024). This complementarity leads to an increase in pollination success and

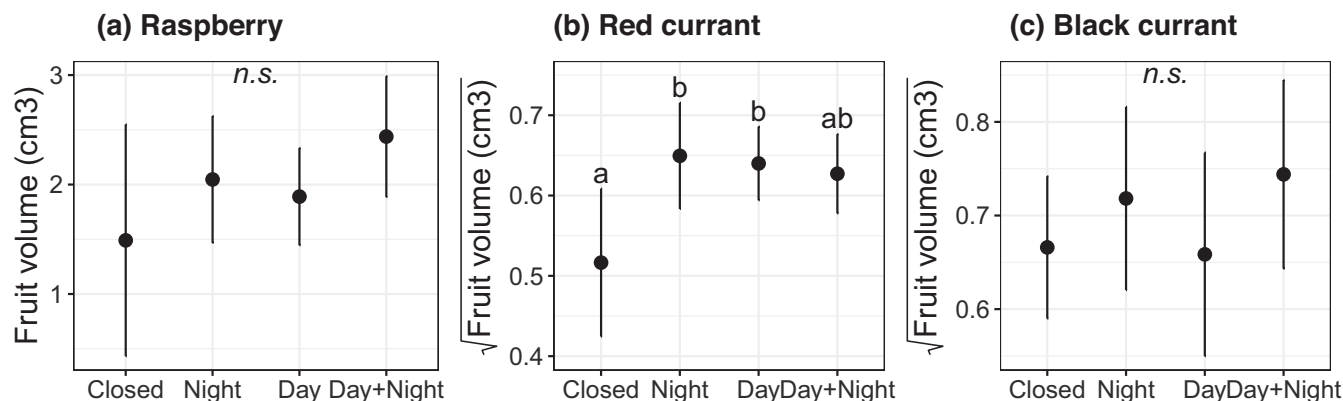


FIGURE 3 | Comparing fruit volume (in cm^3) between Closed, Night, Day and Day + Night pollination treatments in (a) raspberry, (b) red currant and (c) black currant. Dots represent the predicted fruit set per pollination treatments, with thick lines indicating the 95% CI (based on GLM predictions). Different small letters indicate significant differences with a risk of 5%.

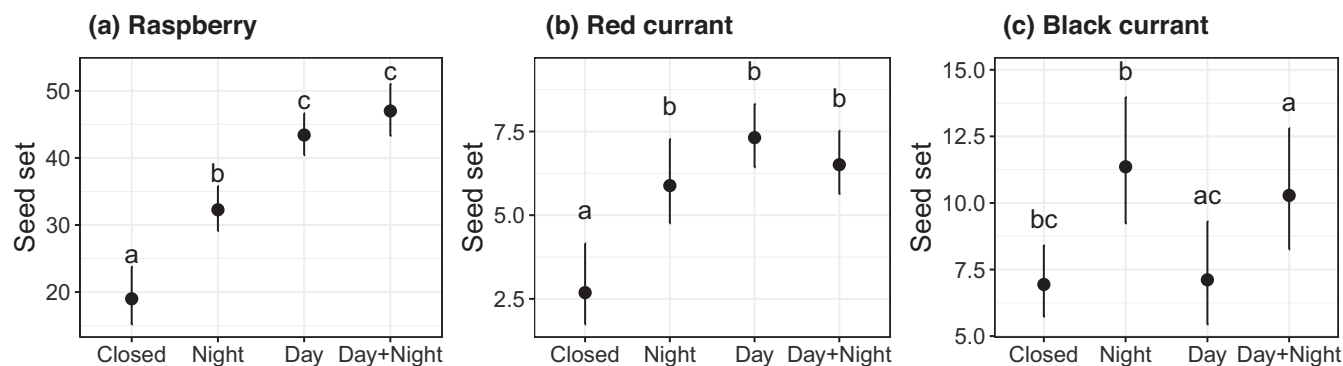


FIGURE 4 | Comparing seed set between Closed, Night, Day and Day + Night pollination treatments in (a) raspberry, (b) red currant and (c) black currant. Dots represent the predicted fruit set per pollination treatments, with thick lines indicating the 95% CI (based on GLM predictions). Different small letters indicate significant differences with a risk of 5%.

thus yield of pollinator dependent crops (Albrecht et al. 2012; Fründ et al. 2013). This also explains why exposure to both diurnal and nocturnal pollinators produces the best results in terms of fruit set for black currant. Our results further suggest that pollination service is higher for diurnal than for nocturnal visits, for raspberry seed set. Our pollinator observations reveal that raspberry flowers received more visits than flowers of the other crops, which could explain why this diurnal pollination service is more pronounced for this crop. Although we were not able to monitor nocturnal pollinators responsible for the reported nocturnal pollination service, we hypothesize that insects such as moths (nocturnal Lepidoptera) and Diptera could have visited flowers of our study crops at night, since these were reported as nocturnal pollinators for bramble, a species of the same genus as raspberry, in the south of England (Anderson et al. 2023). Our study also confirms the benefits of insect-mediated pollination services, for fruit set of all three crops (Klein et al. 2007). In particular, the results highlight the service provided by day-active pollinators, which increased red currant fruit set, seed set and fruit volume, as well as raspberry seed set.

The a posteriori power analysis performed confirmed that the sample size was sufficient to detect nocturnal pollination. Indeed, even though an important number of flowers did not form fruits, the successfully formed fruits had sample sizes above the required threshold for all three crops. We had the smallest sample size for raspberry, the only crop for which the experiment was not replicated a second year. It is worth noting that the power analysis was performed using results from experiments on strawberry, which is less pollinator dependent than the three crops considered here (Klein et al. 2007). Thus, we can expect that relatively small sample sizes could be sufficient. Nevertheless, we suggest that future research on nocturnal pollination in these crops, and in particular for raspberry, be replicated in different years and sites, in order to corroborate our results.

We further found that for black currant, seed set was greater in the Night treatment compared to the Day treatment. This seems to suggest that the nocturnal pollination service is greater than the diurnal pollination service. However, it is worth noting that the black currant fruit set success rate was low, leading to a six-fold reduction in sample size. Although the sample size of remaining fruits is adequate with regard to the power analysis, the main effects of the pollination treatments were filtered out through the fruit set experiment. We did not find any effects of pollination treatment on fruit weight for any of the three crops, and only one difference between treatments in fruit volume, in red currant. This could be due to the fact that seed set is a direct result of ovule fertilisation by pollination (Dafni 1992), whereas weight and size are less directly linked to pollination.

This being a small-scale study, we call for future research to incorporate larger sample sizes, which could allow taking plant identity into account as a random effect, to untangle the effects of treatment and plant individual. Moreover, due to the morphology of the three crops used here, whereby flowers grow in inflorescences, we were not able to apply different treatments within these inflorescences, which would have ensured independence of each fruit. We did however replicate each treatment on inflorescences of different plant individuals. This is a commonly

used method to ensure robustness of results despite potential independence issues (Anderson et al. 2023; Latet et al. 1999; Ryan et al. 2023). Challenges in setting up such a day–night pollination experiment prevented us from replicating the study on different sites within the same year. We were however able to replicate the experiment in 2024 in a different site on black currant and red currant plants. Despite the different conditions between the 2020 and 2024 experiments, the results are comparable since the plants used in 2024 developed from cuttings of those used in 2020. We detected in our results that red currant fruit set, fruit volume and seed set, as well as black currant fruit volume, were greater in 2020 than in 2024. This could be due to weather conditions being more favourable in 2020 (average maximum temperature in May of 24.5°C, with 80.5 mm of rain in the region of the study site (MétéoFrance 2020)) than in 2024 (average maximum temperature in May of 18.6°C, with 141.3 mm of rain in the region of the study site (MétéoFrance 2024)), allowing for more pollinator activity and consequently better fruit development, since pollinators preferentially forage in warm and clear climatic conditions (Tuell and Isaacs 2010). Moreover, since the experiment took place on different sites between years, the sites and their potentially unique pollinator communities may play a role in explaining the difference in yield components. Both study sites were in a mixed landscape, with the first being within a protected area and the second within a suburban area with a forested landscape in the surrounding area. This allowed us to examine the contribution of nocturnal pollinators in favourable conditions for pollinator diversity. Indeed, unfavourable conditions for pollinators in agricultural habitats (Goulson et al. 2015), potentially restricting the presence of nocturnal pollinators, may prevent us from detecting whether they can contribute to pollination services in such landscapes. Future studies could expand upon our observations by examining nocturnal pollination services at larger scales with more plants and sites along a gradient of landscape complexity (i.e., from semi-natural areas to intensive agricultural landscapes) to explore how less favourable conditions for diverse pollinator communities would affect nocturnal pollination services. To overcome this challenge, new technological methods are being developed to allow night-long surveys to be performed, such as automated video (Wonderlin 2023) or photo (Alison et al. 2022) recordings. In particular, one study presents a recently developed camera trap specifically designed to capture plant–pollinator interactions (Droissart et al. 2021). Once the nocturnal pollinator community is characterised, single visit pollen deposition techniques or body pollen counts, widely used in diurnal pollination studies (Bernauer et al. 2022; Földesi et al. 2021) can be co-opted to evaluate nocturnal pollinator efficiencies. Using this method, a recent study demonstrated that pollen deposition at night varies between pollinator taxa, emphasising the importance of understanding the pollinating efficiency of different nocturnal pollinators (Broussard et al. 2022).

Although our experimental sites were not particularly subject to Artificial Light At Night (ALAN) or night-time pesticide application, our findings confirm the need to take nocturnal pollinators into account, and thus to take into account the threats they may face. Indeed, the decline of diurnal pollinators and its causes are well documented (Goulson et al. 2015; Potts et al. 2016). However, since knowledge about nocturnal pollinators is so sparse, threats to them remain largely unknown (Macgregor

and Scott-Brown 2020). One study found that light pollution reduced the amount of pollen transported by moths (Macgregor et al. 2017), and could disrupt nocturnal pollinator networks, with negative effects on plant reproduction (Knop et al. 2017). Research should focus on understanding the effects of ALAN on crop pollination, particularly in areas where light pollution is intense, like cities, since there is an increasing demand for agricultural land to be close to where people live (Mok et al. 2014). A recent study found that urbanisation affects the diversity of pollen transported by nocturnal pollinators (Nicholls et al. 2023). Production of crops grown in urban landscapes will likely be deterred by urbanisation, and in particular by ALAN, which disrupts pollinator communities.

In agricultural landscapes, an additional threat to nocturnal pollinators currently is the application of pesticides at night. Indeed, pesticide guidance labels, government institutions and universities recommend that certain pesticides (especially insecticides) not be applied when bees are active, often recommending application either in the early morning or in the evening (Decourtye et al. 2016; Government of British Columbia, Canada 2012; Karbassioon and Stanley 2023). In particular, in France, the recent update of the “pollinator-friendly” legislation prevents pesticide applications during the day, but allows them at night (Ministère de l’agriculture et de l’alimentation 2021). These recommendations stem from a lack of knowledge of the existence and importance of nocturnal pollinators, reinforcing our argument that more research on nocturnal pollinators is needed to safeguard the pollinators themselves and the valuable pollination services they provide to crops.

5 | Conclusion

In conclusion, our results indicate that nocturnal pollinators provide pollination services to small fruit crops in the context of the study. Moreover, results indicate that both diurnal and nocturnal pollination enhance the potential to maximise crop pollination in red currant and black currant. This may increase fruit production. This study is, to our knowledge, the first to evaluate nocturnal pollination services for these crops, adding to a growing body of evidence that nocturnal insects contribute to crop pollination services. Since nocturnal pollination is understudied, threats to night-active pollinators are poorly described compared to their diurnal counterparts. Thus, we highlight the urgency for nocturnal pollinators to be considered in future research and management practices.

Author Contributions

Conceptualization: F.R. Data Curation: F.R. Formal Analysis: E.B. and F.R. Investigation: F.R. Methodology: F.R. Project administration: F.R. Resources: F.R. Supervision: F.R. Validation: F.R. Visualisation: E.B. and F.R. Writing – Original Draft Preparation: E.B. Writing – Review and Editing: F.R.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Figshare at <https://doi.org/10.6084/m9.figshare.29930195.v1>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supporting Information.