Article

POLLINATOR DEPENDENCE AND POLLINATION DEFICIT IN *HEDERA HELIX*, AND EFFECTS ON FRUGIVORE FEEDING CHOICES

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Abstract—English ivy (*Hedera helix*) is an important resource for wildlife in rural and urban ecosystems. It provides pollen and nectar for flower-visiting insects during autumn and fruits for frugivores during winter and spring. A requirement of insect pollination for fruit set in ivy implies that recent declines in pollinator populations can threaten food supply for frugivores. This study investigated the link between pollination services and the quantity and quality of fruit produced in ivy, and how that could in turn influence frugivore feeding choices, in a mixed woodland and an urban garden habitat respectively. Surveys on pollinator community and activity were conducted to assess the overall level of pollination. A set of experiments involving insect exclusion, open pollination, and extra pollen supplementation was performed to reveal the level of pollinator dependence and pollination deficit in ivy. Additionally, the removal of these fruits by frugivores was measured to test whether frugivore feeding preferences are influenced by the initial level of pollination. Our results showed that the quantity and quality (size) of fruit produced in ivy were significantly reduced under insect exclusion, which is strong evidence for pollinator dependence. Pollination deficit was also identified at both sites. Furthermore, the data indicate that frugivores can display some degree of preference for well-pollinated ivy fruits. Taken together, our study shows that declines in pollination services will have direct impacts on the availability and quality of ivy fruits for frugivores. Maintaining the health of pollinator communities in both urban and rural habitats could therefore ensure healthy ecosystem functioning.

Keywords—Ivy; Pollination services; Pollinator decline; Ecosystem functioning; Species interactions; Frugivory

INTRODUCTION

The role and importance of pollination services is well-recognised for fruit and seed set in food crops (Klein et al. 2007; Ricketts et al. 2008), but much less research effort has been put into studying pollination in ecosystems and plant species occurring in human-influenced landscapes but not directly involved in agriculture, such as English ivy, *Hedera helix* L. (hereafter, 'ivy'), and other hedgerow plants. There is empirical evidence that ivy requires insect pollination service for fruit production (Jacobs et al. 2009), termed "pollinator dependence". It is also common for plant species to suffer from pollen limitation and pollination failure, often caused by insufficient delivery of pollen grains due to low levels of pollination service or lack of pollen donors in the environment (Buchmann & Nabhan 1997; Thomson 2001; Wilcock & Neiland 2002; Ratto et al. 2018), leading to "pollination deficit" which results in sub-optimal fruiting success (Kearns et al. 1998). In addition to fruiting success, research has found that more diverse pollinators and pollination sources are beneficial for the quality of food crop yield, for example in terms of larger fruit size, higher nutritional values, or lower degree of malformities (e.g. Abrol et al., 2019; Dinh Dung et al., 2021; Garratt et al., 2014; Halder et al., 2019; Lata et al., 2018). However, there is little to no information on whether this holds true for ivy or other wild fruit-bearing plants in human-influenced landscapes.

Ivy is an evergreen woody climber native to the UK. It is unique among European fruit-bearing plants in that flowering occurs late in the year during autumn, typically around September to November in the UK (Metcalfe 2005; Vezza et al. 2006). Only mature ivy above ten years of age produces flowers (Clark 1983). Ivy flowers consist of multiple buds clustered together, forming an umbel, with on average six umbels on each flowering shoot (Bottema 2001). Typically, the terminal umbel flowers first and is the only umbel to develop into fruit (Metcalfe 2005). The flowers are hermaphrodite and protandrous, meaning the anthers release pollen before the stigma is receptive (Harris & Harris 2001). The ovary of each flower has five ovules, each of which could form a seed if successfully fertilised through pollination. When flowering, the nectaries are completely exposed to the external environment for visiting insects (Pacini et al. 2003; Konarska 2014).

Ivy provides a succession of resources from autumn to spring, first for insects and then for frugivores. Because ivy flowers relatively late in the year, it serves as an important source of pollen and nectar for flower-visiting insects before they go into hibernation (Garbuzov & Ratnieks 2014). A range of insects are known to forage on ivy flowers, mostly Hymenoptera (bees and wasps), Diptera (true flies) and Lepidoptera (moths and butterflies) (Knuth et al. 1906; Bottema 2001; Ollerton et al. 2007; Jacobs et al. 2010; Garbuzov & Ratnieks 2014). After flowering is completed, flowers that are successfully pollinated develop into fruits, swelling up and blackening into a dark purple colour when mature and fully ripe (Grosbois 1976). Most fruits ripen by March and April, and are consumed by numerous resident and migratory frugivorous bird species from December to May (Snow & Snow 1988; Metcalfe 2005). Birds that have been observed to consume ivy fruits include blackbirds (*Turdus merula*), blackcaps (*Sylvia atricapilla*), woodpigeons (*Columba palumbus*), starlings (*Sturnus vulgaris*), and robins (*Erithacus rubecula*) (Sorensen 1981; Snow & Snow 1988; Hernández 2005; Jacobs et al. 2010; Galimberti et al. 2016). These fruits represent a nutritious food resource in winter and spring for frugivores, as they have a high lipid content in their pulp (Grosbois 1976; Metcalfe 2005).

Under anthropogenic impacts such as land-use change, habitat fragmentation and agricultural intensification, there is increasing evidence that pollinating insects are now in decline both in the UK and the rest of the world (Biesmeijer et al. 2006; Kosior et al. 2007; Winfree et al. 2009; Potts et al. 2016). However, some forms of land use change, such as urbanisation, have been found to have potential positive influences on pollinator communities (Baldock et al. 2015; Kaluza et al. 2016; Wenzel et al. 2020). For example, urban greenspaces could contain a high diversity and density of flowers which provides habitat opportunities and food resources for pollinators (Hall et al. 2017; Daniels et al. 2020).

Given that ivy is abundant and well-distributed in both rural and urban areas throughout most of the British Isles and across south-western Europe (Metcalfe 2005; Garbuzov & Ratnieks 2014), and that it is a crucial resource to both flower-visiting insect and frugivorous species at separate times of the year, reductions in quantity and quality of fruit set caused by pollinator declines could have ramifying effects throughout these ecosystems. As a result, it is important to understand how ivy fruit production is influenced by pollination services in the context of both rural and urban habitats, as well as the potential consequences on frugivore food supply under future pollinator decline.

The current study intends to investigate the link between pollination service and the quantity and quality of fruits produced in ivy, and how that in turn affects feeding choices in frugivores. This study was carried out in a mixed woodland-meadows nature reserve and an urban botanical garden to allow comparisons across the two habitat types. Particularly, the following questions were addressed:

1. Does the pollination service provided by insects differ between the woodland and urban garden habitat?

2. How pollinator dependent is ivy?

3. Is there a pollination deficit for ivy in these two habitat types?

4. Does the level of pollination affect frugivore preference for the fruits produced?

Pollinators are known to be heavily influenced by microclimatic conditions in the habitat (Bates et al. 2011; Fenoglio et al. 2021), and because urban gardens and woodlands differ in their vegetation structure and assemblage of plant species, it is expected that the pollinator community would differ, leading to unequal pollination services in the two habitat types. To investigate the level of pollinator dependence and pollination deficit in ivy, a set of pollination experiments involving pollinator exclusion, open pollination, and manual cross-pollination was conducted. Fruit set of ivy was previously found to be significantly correlated with insect visitation rates (Jacobs et al. 2009), so it is predicted that under pollinator exclusion, the quantity as well as the quality of ivy fruits would be reduced. On the other hand, the presence and level of the pollinator deficit is likely to vary between habitat types with the pollination service provision. Lastly, if higher levels of pollination enable fruits of greater size and quality to be produced, it is expected that frugivores would prefer these higher quality fruits over those that were produced under lower levels of pollination.

MATERIALS AND METHODS

STUDY SITES

This study took place at Trumpington Meadows (52.1733° N, 0.1054° E) and the Cambridge University Botanic Garden (52.1936° N, 0.1273° E) in Cambridgeshire, UK. Trumpington Meadows represents a mixed woodland and wild meadows habitat. It is a 58-hectare nature reserve managed by the Wildlife Trust for Bedfordshire, Cambridgeshire and Northamptonshire (Wildlife Trust BCN 2018) and is located around 4.8 km south of the Cambridge city centre, alongside the River Cam and Bryon's Pool Local Nature Reserve. The Cambridge University Botanic Garden (hereafter, 'Botanic Garden') represents an urban garden habitat. It is a botanical garden operated by the University of Cambridge, located adjacent to the city centre of Cambridge. The garden covers around 16 hectares of land and holds a plant collection of over 8000 species (Cambridge University Botanic Garden 2021).

POLLINATOR SURVEYS

Surveys of pollinator activity on ivy flowers were conducted between 26 September-12 October 2021. These surveys followed the 'Flower-Insect Timed Count' (FIT Count) protocol from the UK Pollinator Monitoring Scheme (UK Pollinator Monitoring Scheme 2021), which involved counting and identifying pollinators landing in a 50×50 cm quadrat for ten minutes. The number of ivy umbels contained in each quadrat was counted beforehand. These surveys were all carried out between 10 a.m. and 3 p.m. under specific conditions: dry weather, clear skies (less than 50% cloud coverage), mild wind conditions (leaves remained still or only moving gently), and temperatures above 15°C. The sky and wind conditions were observed and documented during the survey. Temperature was measured with a digital temperature probe positioned adjacent to ivy flowers before the survey. A total of 12 and ten pollinator surveys were carried out at Trumpington Meadows and the Botanic Garden respectively, where quadrats were placed within one metre of the ivy flowers involved in the pollination experiment (described in the next section) (details on pollinator surveys: Appendix Tab. S1). The identities of the visiting insects were recorded to the level of morphospecies, which were then categorised into eight broad taxonomic groups as outlined by the FIT Count protocol: bumblebees, honeybees, solitary bees, wasps, hoverflies, other flies, butterflies and moths, and insects smaller than 3 mm (see Appendix Tab. S2 for examples). Proportions of each insect group contributing to the overall flower visitation was calculated to represent the pollinator community of ivy flowers present at each site. To assess completeness of sampling of the pollinator community, species accumulation curves and sample coverage curves were constructed using the "iNEXT" package in R (Hsieh et al. 2016).

POLLINATION EXPERIMENTS

Pollination experiments and treatments were set up and performed between 25 September-14 October 2021. Ivy plants were selected at random at the two sites, with 12 plants at Trumpington Meadows and ten plants at the Botanic Garden (details on location of replicates: Appendix Tab. S3), although sample sizes in later analyses were smaller due to wind damage. For each plant, three separate shoots that were not yet in flower were chosen and marked with coloured tape. One of three treatments was then applied to their terminal

umbels, while the other non-terminal umbels on the selected shoot were removed. This was to prevent abortion of the terminal umbel and reallocation of resources to the non-terminal umbels during the experiment. The three treatments were: 1) Bagged – the umbel was enclosed in a 20x30 cm bag made of 1 mm nylon mesh for the whole duration of flowering to exclude all insect visitors; 2) Open – the umbel was left untreated in the open and could be freely pollinated by flower-visiting insects; and 3) Hand Pollinated (HP) – pollen supplementation through manual cross-pollination was carried out in addition to being fully exposed to insects as in the open treatment.

Pollen for manual cross-pollination in the HP treatment was freshly obtained from flowers of at least three separate individual ivy plants to ensure viability. Each donor plant was located over 10 m away from the treated plant. A small paintbrush was used to collect pollen from the anthers of donor flowers and transferred to the recipient flower by brushing over its stigma. For each umbel in the HP treatment, hand pollination was carried out every other day for a total of three rounds, with the first round starting one day into flowering. This was to maximise the delivery of pollen grains within the three days of stigma receptivity following flowering (Vezza et al. 2006).

MEASURING FRUITING SUCCESS AND FRUIT QUALITY

Towards the end of the flowering period in late October, the number of flower buds in each umbel was counted for all treatments. The flowers were then left to develop into fruits in the field, with mesh bags placed over all treatments to prevent predation on the developing fruits. Flowers with no successfully fertilised ovules would likely be abscised and would not develop into mature fruits (Jacobs et al. 2009; Jackson et al. 2011).

Later in the season (late December to early February), the number of ivy flowers that successfully developed into mature and fully ripened fruits (i.e. of a dark purple colour and spherical in shape) was counted for every umbel in each treatment. Percentage of flowers that successfully set fruit was then calculated to reflect fruiting success under each treatment.

As a proxy for fruit quality, measurements of fruit size were taken. This proxy was chosen as it

creates minimal damage to the ivy fruits so that it does not affect their consumption by frugivores. A random subset of five fruits from each umbel were chosen and their diameters were measured using vernier callipers with a reading error of 0.05 mm. Eight groups of umbels across both study sites had fewer than five mature fruits produced and in these cases measurements of all fruits were taken.

REMOVAL OF FRUITS

After data on fruiting success and fruit size were collected, the mesh bags were removed and the fruits were left exposed in the field. Each group of fruits was revisited every other day for two weeks, and the number of mature fruits remaining was counted each visit. Survival time of each fruit was then quantified as the number of days it remained until it was last seen. This took place over January 2022 at Trumpington Meadows and mid-February to March 2022 at the Botanic Garden.

STATISTICAL ANALYSIS

To understand site differences in the number of pollinator visits recorded, two Generalised Linear Models (GLMs) were used. The response variable for each GLM was 1) the number of visits by all insects and 2) by wasps exclusively, as wasps are thought to be the most effective pollinators of ivy (Jacobs et al. 2010). Site (Trumpington Meadow or Botanic Garden) was included as the explanatory variable. To control for varying number of ivy umbels included in each pollinator survey, the number of umbels was included as an offset term. The GLM for visits by all insects followed a Poisson error structure with a log-link function, whereas the GLM for wasps-only visits followed a negative binomial error structure instead with a log-link function due to over-dispersion.

To compare pollinator communities between sites, differences in proportions of pollinator groups representing the pollinator community were compared using a Fisher's Exact Test. Monte Carlo simulation was applied to obtain the final *P*-value in order to reduce the computational power required.

To analyse differences in fruit set and fruit size across sites and pollination treatments, we fitted two GLMs. The response variable for each GLM was 1) fruit set, expressed as the proportion of flowers that successfully set fruit for each umbel,

and 2) fruit size, which was the average diameter (in mm) of a random subset of five ivy fruits from each umbel. For both GLMs, the explanatory variables included in the saturated models were site (Trumpington Meadows or Botanic Garden), pollination treatment (Bagged, Open, or Hand pollinated), and the interaction of site with treatment. The interaction term enabled testing of whether ivy plants had the same extent of pollinator dependence and pollination deficit across sites. The GLM for fruit set followed a quasibinomial error structure with a logit-link function. A Gaussian error structure was used for the GLM for fruit size. To produce the final minimal models, backwards stepwise elimination was carried out by comparing the models before and after a single term deletion using a likelihood ratio test. If there was no significant difference in the fit of models (i.e. $P > 0.05$), the term was removed. Post-hoc Tukey's HSD Tests using the 'multcomp' package in R (Hothorn et al. 2008) were then carried out for multiple pairwise comparisons between the three treatments and between sites.

To compare consumption of ivy fruits produced under different treatments, survival analysis using the Kaplan-Meier method (Kishore et al. 2010) was performed on the survival times of fruits, which reflects the feeding choice and preference of frugivores. This was repeated for both study sites. A log-rank test was subsequently carried out to identify any statistical differences among the survival of different treatment groups (Stel et al. 2011). This part of the analysis was done using the 'survival' package in R (Therneau 2022). The 'survminer' package (Kassambara et al. 2021) was used to construct the Kaplan-Meier curves.

All data were analysed in R version 4.2.1 (R Core Team 2022). Assumptions of all statistical tests and analyses were checked and reasonably well-met in the dataset before analyses were conducted. All values given in the text are means ± standard error, unless otherwise stated.

RESULTS

POLLINATOR VISITS

The number of visits by all insects, measured over the span of ten minutes, was higher at Trumpington Meadows (16.5 ± 1.76) than at the Botanic Garden (14.3 ± 0.99) (Fig. 1A). There was

only moderate statistical support for the effect of site on the number of visits by all insects ($z = -1.88$, $P = 0.060$) after accounting for the number of umbels in each observation (Appendix Tab. S4a). Similarly, the number of visits by wasps only, measured over the span of ten minutes, was higher at Trumpington Meadows (16.5 ± 1.76) than at the Botanic Garden (14.3 ± 0.99) (Fig. 1B). The effect of site was not significant on the number of visits by wasps only ($z = -0.64$, $P = 0.520$) after accounting for the number of umbels in each observation (Appendix Tab. S4b).

POLLINATOR COMMUNITY

Species accumulation curves indicated a higher degree of incomplete sampling at the Botanic Garden, but sample coverage was high for both sites (Trumpington Meadows: 98.01%; Botanic Garden: 96.51%), so overall sampling completeness was deemed acceptable (Appendix Fig. S1). We observed a higher proportion of honeybees, wasps, and hoverflies at Trumpington Meadows, while proportions of solitary bees and other flies were higher at the Botanic Garden. Overall, the proportions of insect pollinators from each group were found to be significantly different between the two study sites ($P = 0.021$) (Fig. 2).

FRUITING SUCCESS

The percentage of ivy flowers that produced fruit was related to pollination treatment ($F = 160.07$, d.f. = 2, $P < 0.001$), with no significant effect of site ($F = 0.03$, d.f. = 1, $P = 0.875$) or interaction between site and treatment ($F = 0.64$, d.f. = 2, $P = 0.531$) (Appendix Tab. S5). Percentage of fruit set was the highest under the HP treatment (88.99% ± 2.34), meaning flowers that received extra pollen supplementation in addition to insect pollination yielded the greatest fruiting success. This was followed by flowers that were insect pollinated (Open: 65.02% ± 3.59), and flowers that were excluded from insect pollination had the lowest percentage of fruit set (Bagged: 6.56% ± 1.71) (Fig. 3). Altogether, compared to the open pollination treatment, fruiting success decreased significantly by 89.9% in the absence of insect pollination (Bagged: $P < 0.001$), while extra pollen supplementation increased fruiting success significantly by 36.9% (HP: $P < 0.001$). Fruiting success under the bagged treatment was 92.6% lower than that of the HP treatment ($P < 0.001$) (Appendix Tab. S6).
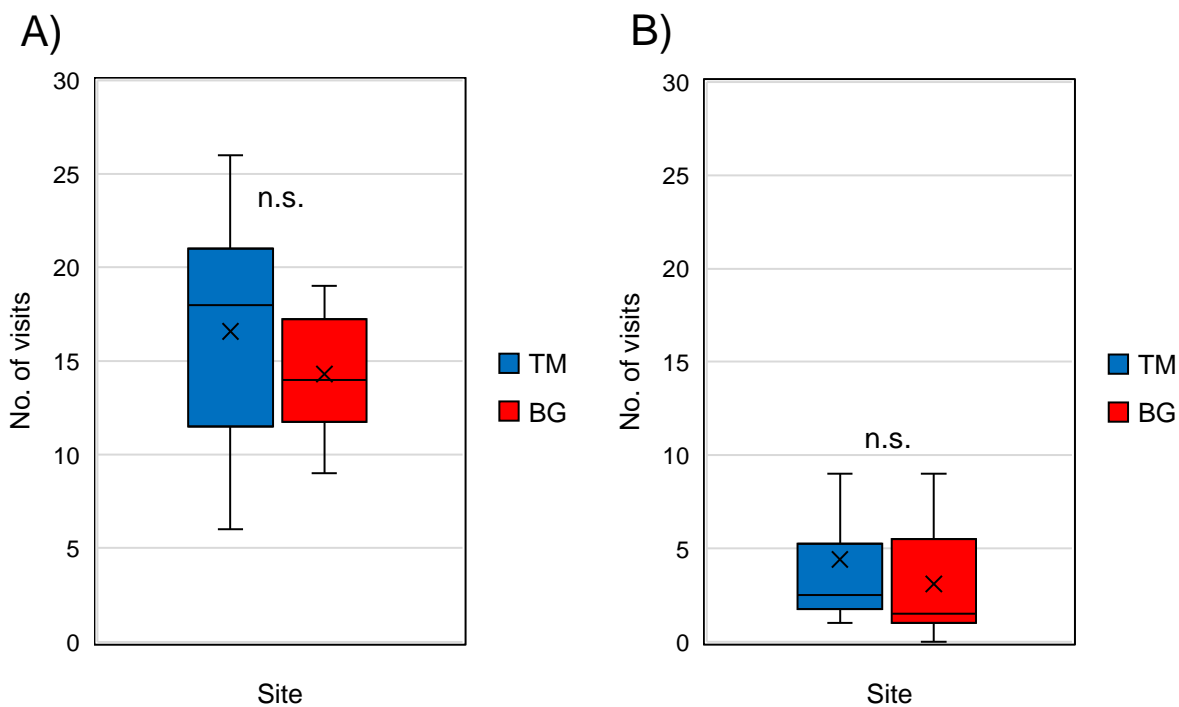
A)

B)

Figure 1. Number of pollinator visits, measured over ten minutes, at Trumpington Meadows (TM, blue) and Botanic Garden (BG, red). Box plots represent medians (central horizontal line) and first and third quartiles (box perimeters). Cross (x) denotes mean. n.s. = not significantly different. A) Number of visits by all recorded insects. B) Number of visits by wasps exclusively.
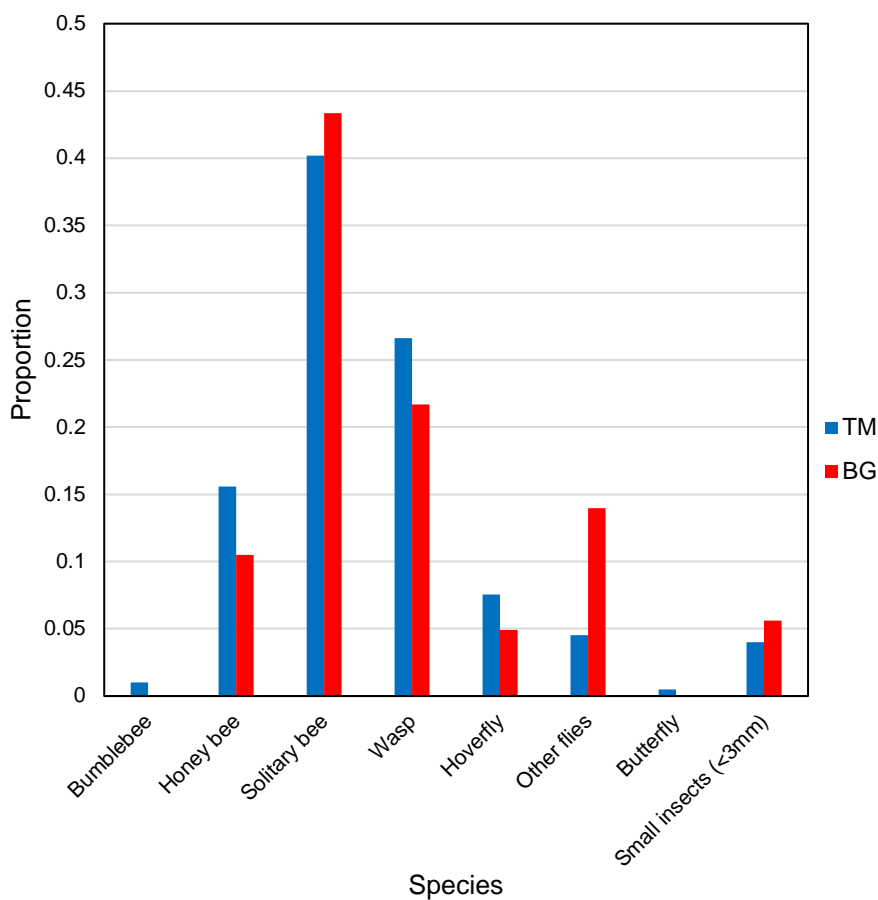

Figure 2. Proportions of pollinator groups recorded at Trumpington Meadows (TM, blue) compared to the Botanic Garden (BG, red). These were found to differ significantly ($P = 0.021$) using a Fisher's Exact Test with Monte Carlo simulation applied.
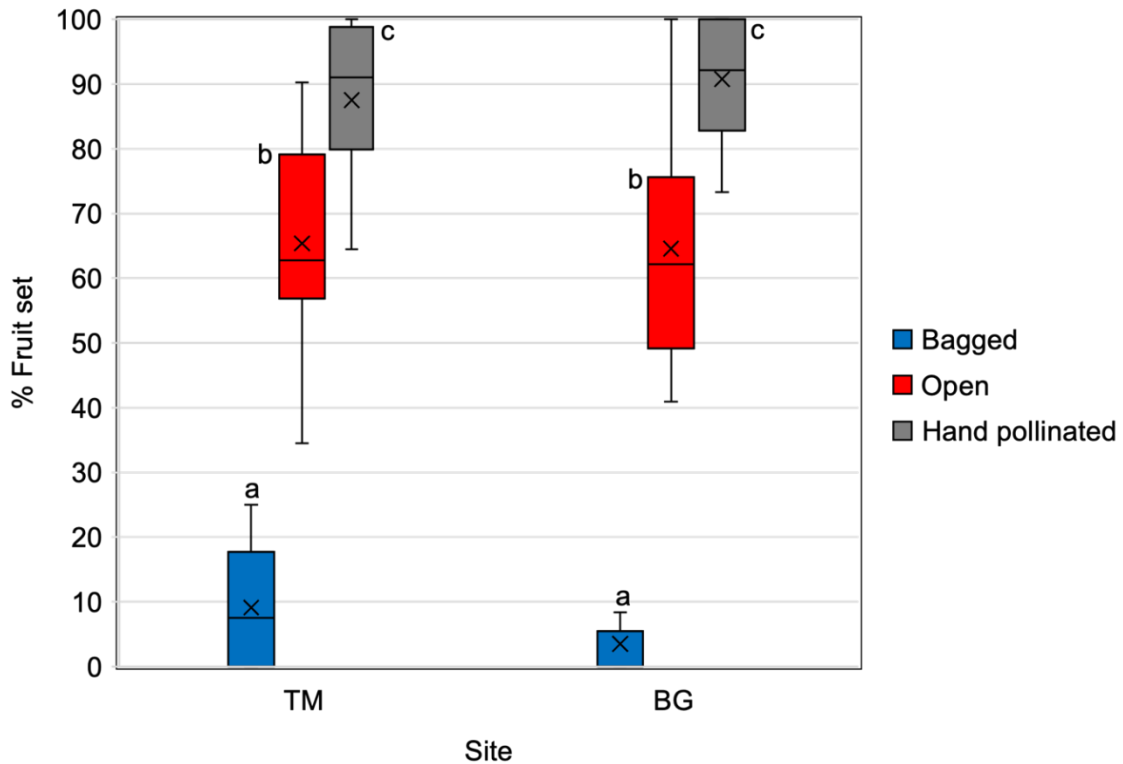
Figure 3. Fruiting success at Trumpington Meadows (TM) (*N* = 12) and the Botanic Garden (BG) (*N* = 10) under different pollination treatments: bagged (blue), open (red) and hand pollinated (grey). Box plots represent medians (central horizontal line) and first and third quartiles (box perimeters). Cross (x) denotes mean. Different letters show significant differences among treatments (a, b, c). Within the same treatment, there was no significant difference between the two sites.
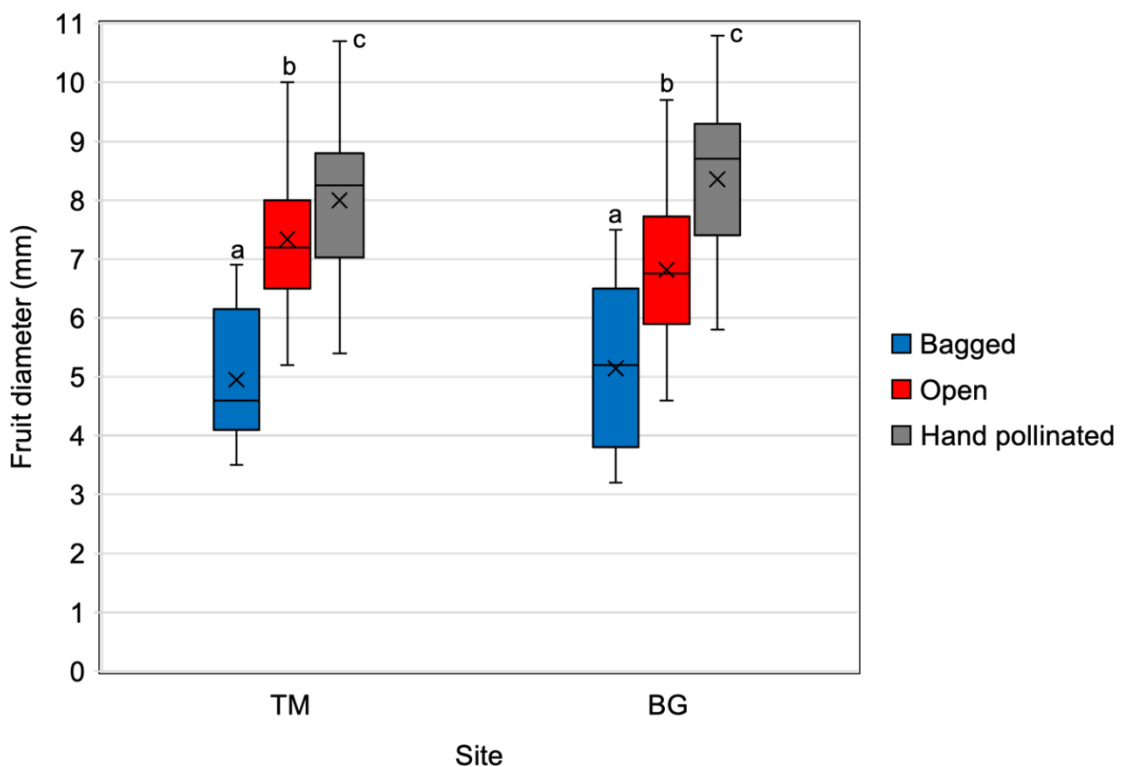

Figure 4. Fruit size at Trumpington Meadows (TM) (*N* = 28) and the Botanic Garden (BG) (*N* = 24) under different pollination treatments: bagged (blue), open (red) and hand pollinated (grey). Box plots represent medians (central horizontal line) and first and third quartiles (box perimeters). Cross (x) denotes mean. Different letters show significant differences in fruit size among treatments within sites (a, b, c). Within the same treatment, there was no significant difference between the two sites.

FRUIT SIZE

Mean fruit size was dependent on the pollination treatment ($F = 41.98$, d.f. $= 2$, $P < 0.001$), with no significant effect of site ($F = 0.84$, d.f. $= 1$, $P = 0.364$) or interaction between site and treatment ($F = 1.12$, d.f. $= 2$, $P = 0.336$) (Appendix Tab. S7). Flowers that were pollen-supplemented produced the greatest mean fruit diameter (HP: 8.12 mm ± 0.12), which was significantly larger than those that were insect pollinated (Open: 7.08 mm ± 0.12) by 14.7% ($P < 0.001$) and pollinator excluded (Bagged: 5.00 mm ± 0.19) by 62.4% ($P < 0.001$) (Fig. 4). Mean fruit diameter under the open treatment was also significantly larger than the bagged treatment by 41.6% ($P < 0.001$) (Appendix Tab. S8).

SURVIVAL ANALYSIS

At Trumpington Meadows, the survival rate of fruits after 14 days was the highest for those that were produced under pollinator exclusion (Bagged: 60.00% ± 8.94), followed by those under insect pollination (Open: 8.57% ± 2.12). Survival rate was the lowest for fruits that were produced under the pollen-supplemented treatment (HP: 0.93% ± 0.65), nearly 65 times lower than the survival rate of pollinator excluded fruits (Fig. 5A). Log-rank analysis showed that the survival rates of fruits under each treatment were significantly different from each other (χ^2 (2, $N = 421$) $= 89.7$, $P < 0.001$), indicating that frugivores showed a preference for fruits produced under higher levels of pollination.

At the Botanic Garden, the overall survival rates of fruits after 14 days were similar for the pollinator excluded (Bagged: 15.38% ± 10.0), insect pollinated (Open: 15.74% ± 3.23), and pollen-supplemented treatment (HP: 6.22% ± 1.74) (log-rank test: χ^2 (2, $N = 333$) $= 3.1$, $P = 0.210$) (Fig. 5B), indicating no observable feeding preference from frugivores towards fruits from different treatments.

DISCUSSION

We found that the pollinator community at the woodland and urban garden study sites were dissimilar, but the number of pollinator visits by all insects or by wasps exclusively was not significantly different between these two sites. Pollinator dependence of ivy was confirmed in this study, as evidenced by the dramatic reduction (89.9%) in fruiting success when insect pollinators were excluded. Additionally, we found that the quality of ivy fruits was also dependent on insect pollination, since fruit size was significantly larger when flowers received insect pollination. This study also found evidence for a pollination deficit in ivy plants at the two study sites, as shown by increases in both fruiting success and fruit size when insect pollinated flowers were supplemented with extra pollen. Survival analysis showed that survival rates of fruits were different among pollination treatments at the woodland study site, with the lowest survival rate for pollen supplemented fruits and highest survival rate for pollinator excluded fruits. This indicates that frugivores differentially fed more on fruits that were pollen supplemented, followed by those that received insect pollination, with the lowest preference for pollinator excluded fruits. However, this pattern was not found in the urban garden habitat.

The difference in pollinator community found between the woodland and urban garden study site is consistent with other research findings. Our small number of study sites limits our ability to infer whether the observed difference in pollinator community is associated with urbanisation. However, numerous studies have found that urbanisation is associated with a change in pollinator community composition, both in terms of species richness and species abundance (Bates et al. 2011; Fortel et al. 2014; Persson et al. 2020). These community changes are likely driven by the availability and variety of floral and nesting resources present at the site (Baldock et al. 2015; Cariveau & Winfree 2015; Hall et al. 2017; Theodorou et al. 2020). Botanical or residential gardens, allotments, and vacant land in urban areas typically contain a high diversity and density of both native and non-native flowers, and therefore can provide more heterogeneous nesting sites and food resources (Hennig & Ghazoul 2012; Theodorou et al. 2017). As a result, these habitats can support a greater diversity of pollinators (Gardiner et al. 2013; Baldock et al. 2019). We might therefore expect pollinator species richness to be higher at the urban garden study site compared to the woodland habitat, which can be assessed in future studies with more extensive pollinator surveys carried out at higher taxonomic resolutions. More study sites for each habitat type
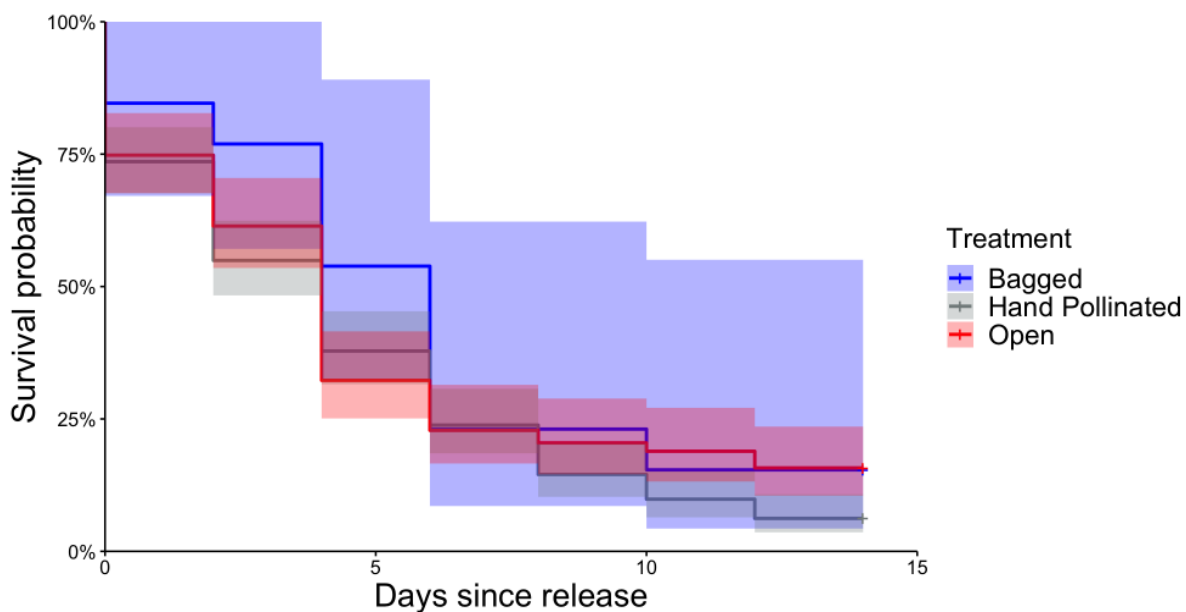
Trumpington Meadows
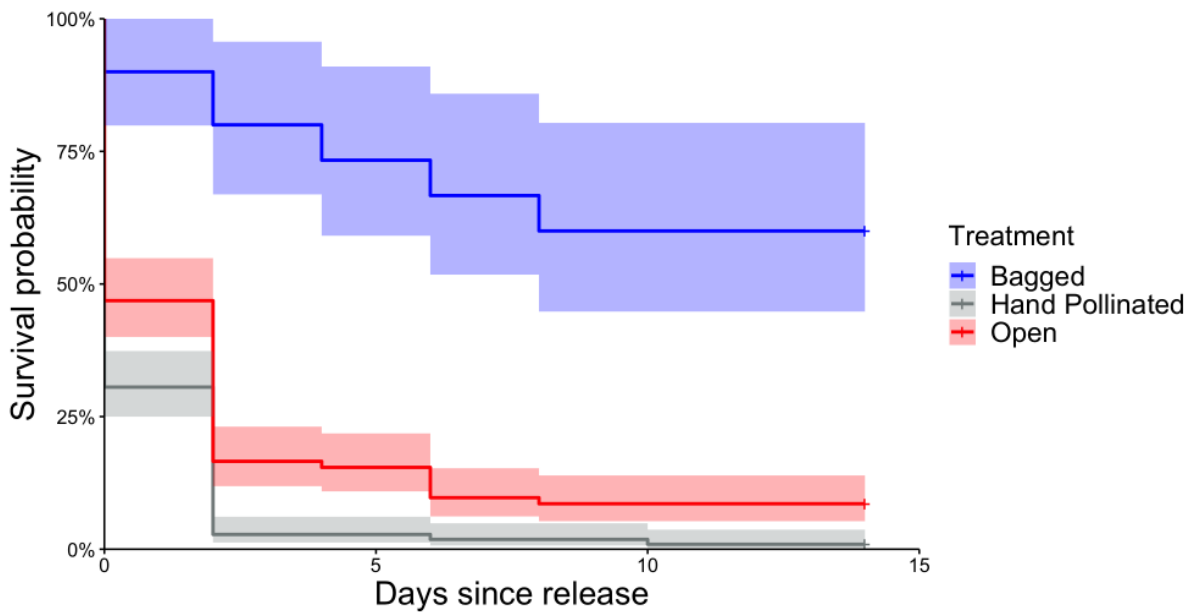
Botanic Garden

Figure 5. Kaplan-Meier survivorship curves for each pollination treatment (shown in different colours) with 95% confidence intervals (shaded areas). Day zero refers to the day when the fruits were first released. At Trumpington Meadows, overall survival probability at the end of 14 days was 0.926%, 8.57% and 60.0% for the hand pollinated (*N* = 216), open (*N* = 175), and bagged (*N* = 30) treatment respectively. Log-rank test showed that the three curves are significantly different (*P* < 0.0001). At the Botanic Garden, overall survival probability at the end of 14 days was 15.4%, 15.7% and 6.22% for the hand pollinated (*N* = 193), open (*N* = 127), and bagged (*N* = 13) treatment respectively. Log-rank test showed that the three curves are not significantly different from each other (*P* = 0.210).

are also necessary for our study to draw conclusions about whether urbanisation is driving the difference in pollinator community.

Despite having different pollinator communities, our results suggest that the pollination service to ivy flowers was similar across the two study sites. We expected that the pollination service would differ between sites due to their non-identical pollinator communities. This is because the functional traits of a given pollinator species could affect its effectiveness at carrying and transferring pollen (Garibaldi et al. 2013). For

example, pollinator hairiness could determine the level of pollen deposition during a visit (Stavert et al. 2016). Correspondingly, pollinator communities with different species compositions are not all equally effective at pollinating a specific plant species (Willcox et al. 2017). However, we found that fruiting success and fruit size did not differ significantly between our two study sites. We hypothesise that this is because the two study sites had comparable pollinator visitation, particularly for wasps, which were suggested to be the most effective pollinators of ivy (Jacobs et al. 2010). Additionally, higher visitation by honeybees and hoverflies in Trumpington Meadows and higher visitation by solitary bees and other flies at the Botanic Gardens may have resulted in similar levels of pollination for ivy overall. If this were the case, then the two pollinator communities with different taxonomic group compositions could be considered as functionally equivalent. Individual pollinator efficiency would need to be studied further to determine which species are more efficient at pollinating ivy.

On the account of time and weather constraints, only a limited number of pollinator surveys were carried out from late September to early October for the current study. However, abundance and diversity of pollinators visiting ivy flowers could potentially display temporal variation within the season over longer time spans (e.g. Crall et al., 2020; McCall & Primack, 1992), which could have significant impacts on pollination level of ivy that was not captured in this study.

This study also provides clear evidence that ivy requires insect pollination, confirming the results from previous research (Jacobs et al. 2009). Exclusion of pollinators led to approximately 90% reduction in fruit set, which categorises animal pollination as 'essential' for ivy fruit production according to Klein et al. (2007). We also found that insect pollination could impact the size of fruits produced, indicating that quality of fruits in wild fruit-bearing plants could be affected by the level of pollination service provided. Without any exposure to pollinators, ivy plants were still able to produce a low level of fruit set, but these fruits were smaller compared to those that received pollination. These results reiterate how crucial animal pollination service is not only to crop production and agricultural productivity, but also to wild flowering plants (Ollerton et al. 2011; Rodger et al. 2021; Katumo et al. 2022). Pollinator declines can therefore have a large impact on the total volume of fruit produced, threatening food supply to frugivores.

Pollination deficit was also demonstrated in ivy plants at both study sites. Extra pollen supplementation led to increased fruit set by around 37%, as well as further increases in fruit size. This indicates that the total level of pollination at these sites was insufficient to reach the maximal level of fruit set and fruit size, which could have been caused by a range of factors. Insufficient levels of effective pollination, either caused by low frequencies of insect visitation or lack of effective pollinators, could lead to failure in pollen dispersal, thus resulting in sub-optimal fruit production (Thomson 2001). Moreover, the lack of viable pollen donors in the environment could also lead to insufficient pollination, contributing to the pollination deficit (Ratto et al. 2018). When density or population size of the target plant species is low or restricted, it could limit the quantity of viable conspecific pollen that is delivered (Wilcock & Neiland 2002), such that not all available ovules are fertilised and the total percentage of fruit set is below the maximum. Long periods during transport of pollen could also result in pollen being inviable upon reaching a conspecific plant (Wilcock & Neiland 2002). This could be the case at the urban garden study site, where casual observations suggest mature ivy plants were less abundant and more spaced out throughout the site because they were regularly managed and chopped down. However, at the woodland habitat, ivy flowers were more abundant and densely populated along the tree line. For that reason, lack of pollen donors in the environment is less likely to be the cause of pollen limitation at this site. Instead, pollination deficit may be caused by insufficient pollination services by pollinators. This also illustrates that the presence and causes of pollination deficits are highly context-dependent and ivy plants in other sites might not suffer from such limitations. As suggested by Thomson (2001), longer-term studies over several seasons at the study sites would be needed to determine whether such pollination deficits are chronic, which would then imply there has been a recent decline in pollination services. Extending the research to

cover more sites of varying pollinator diversity and density, as well as ivy abundance and density, could help further examine the causes of pollination deficit at different locations.

Regarding survival of ivy fruits, we found that the level of consumption, hence preference, for fruits that received different levels of pollination was not equal at the woodland site. Preference and consumption of pollen-supplemented fruits was the highest, with less than 1% of the fruits remaining after 14 days, while fruits that did not receive any insect pollination had over 50% remaining over the same time span. Although our dataset is limited in size, this is still an indication that frugivores can show stronger preferences for larger fruits. Our study did not analyse other measures of fruit quality, such as fruit weight, acidity level, sugar concentration, or lipid content. However, it is highly plausible that these other measures of fruit quality would also be enhanced when flowers were exposed to greater levels of pollination, as seen in many food crops (e.g. Klatt et al., 2014; Samnegård et al., 2019). Therefore, the initial level of pollination received by ivy flowers not only affects the quantity and quality of fruits produced, but also has influences over frugivore foraging choice and behaviour.

Contrastingly, there were no clear trends in preference for fruits produced under different pollination treatments at the urban garden site. Several factors may explain this discrepancy. First, difference in diversity and density of the frugivore community at each site could lead to different foraging patterns. As seen from the pollinator community, urbanisation can dramatically alter the composition and diversity of organisms present (Concepción et al. 2015; Callaghan et al. 2018), often favouring bird species that are less sensitive to human disturbance, which tend to be generalists (Kark et al. 2007; Bonier et al. 2007; Evans et al. 2011). Consequently, it is possible that bird species present in the urban garden habitat were less selective and consumed fruits regardless of their quality. Alternatively, frugivores at the urban garden site might not have exhibited any clear feeding preference due to greater competition. Abundance and density of these urban-tolerant generalist birds has been shown to increase with urbanisation (Chace & Walsh 2006; van Heezik et al. 2008). Observations also suggest

that availability of ivy fruits was lower at this site since ivy was less abundant. As a result, there might have been more competition both within and among species at the urban garden site and so frugivores were less selective and consumed fruits even if they were of lower quality. A final possible theory to explain the occurrence of feeding preference at the woodland site but not the urban site is that frugivore species might impose a threshold for fruit size, below which they would ignore and not consume the fruit. From our dataset, this size threshold could be about 5mm in diameter. Fruits from the insect exclusion treatment were the smallest at both sites, but the median and mean fruit diameter at the urban garden were both above 5mm, whereas those at the woodland site were below. If the proposed size threshold existed, a greater proportion of fruits from this treatment at the garden site were above it, which explains why they were consumed to a greater degree, leading to less distinct preferences for fruits produced under different pollination treatments overall. Presence of a fruit size threshold for food selection in frugivores emphasises the importance of pollination services, as insect pollination increases both fruiting success and sizes of fruits significantly, thus maintaining or even increasing the supply of fruits preferable to frugivores.

CONCLUSION

The significant decrease in fruiting success and fruit size in ivy, observed when pollinators were excluded, emphasises the plant's strong dependence on pollinators. Declines or changes in pollinator community in an ecosystem could diminish effective pollination, which might then reduce the total pollination services provided. This will potentially lead to greater pollination deficits for ivy, which is shown to result in sub-optimal fruit set and fruit size. This study shows that frugivore species may exhibit preferences for higher quality or larger fruits, potentially with a size threshold for selection. Therefore, pollinator declines leading to reduced ivy fruit quantity and quality could be detrimental for the frugivore community by impacting their food supply. Accordingly, maintaining the health of pollinator communities in the ecosystem is crucial to provide reliable pollination services and ensure consistent supply of high-quality ivy fruits for frugivores.

Future research should extend the study to other common wild fruit-bearing plants, so that we may gain a more comprehensive picture of the impact of pollinator declines on fruit resources available for frugivores.

AUTHOR CONTRIBUTION

Concept and design ML & LVD, data collection ML, data analysis ML, IR & LVD, writing ML, edits and approval for publication IR & LVD.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

DATA AVAILABILITY STATEMENT

The complete R code along with all supporting datasets can be found at https://zenodo.org/doi/10.5281/zenodo.10501296.

APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. Details on pollinator surveys.

Table S2. Details on ivy replicate locations.

Table S3. Results of Generalised Linear Model for fruiting success.

Table S4. Results from Tukey's HSD Tests for multiple comparisons of means for fruiting success.

Table S5. Results of Generalised Linear Model for fruit size.

Table S6. Results from Tukey's HSD Tests for multiple comparisons of means for fruit size.

Figure S1. Species accumulation curves and sample coverage curves from pollinator surveys.

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