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Climate impacts apple pollination, yield and economic outcomes of farmers

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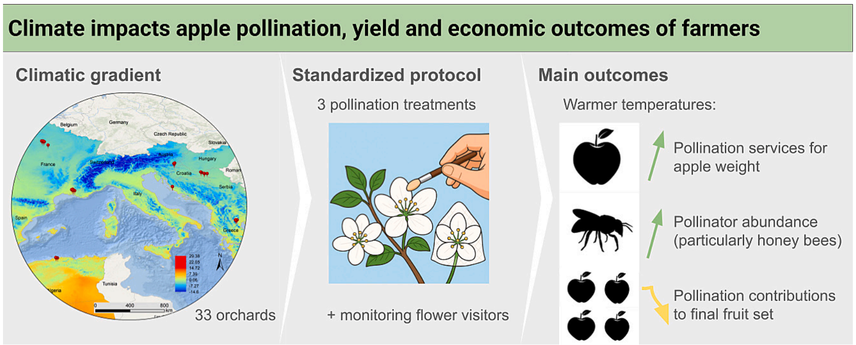
HIGHLIGHTS

- Climate dependence of crop pollination remains poorly understood
- Flower visitors, especially honey bees, are more abundant in warm local temperatures
- Economic benefits increase with temperature, but the role of pollinators decreases
- Wind-mediated pollination and orchard management practices may support apple yield
- Findings highlight need for climate-resilient strategies in agriculture

GRAPHICAL ABSTRACT



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ABSTRACT

Animal-mediated pollination is crucial to global food production but is increasingly threatened by environmental degradation, habitat loss and climate change. The extent to which temperature affects pollination services and crop yields is poorly understood. Using standardised monitoring in 33 apple orchards across Europe and Northern Africa over two years, this study assessed how ambient temperature affects flower visitors, fruit set, fruit quality and economic outcomes. Observation-time warm temperatures increased pollinator abundance, particularly of honey bees, while long-term mean annual temperatures enhanced pollination services for apple weight. Apple yield and the economic benefits to farmers increase with temperature, while the role of pollinators decreases along the climatic long-term mean annual temperature. These important findings suggest that another process may be at play beyond animal-mediated pollination. It was hypothesised that wind-mediated pollination may occur preferentially in Mediterranean regions, where farmers adapt their management strategies to benefit

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from this service. These results highlight the effects of climate change on agricultural production, the economic outcomes of farmers and food security and emphasise the need for climate-resilient strategies to support animal-mediated pollination and other ecosystem services.

1. Introduction

Animal-mediated pollination is critical for global food production, with insects playing an important role in performing cross-pollination (Aizen et al., 2009; Klein et al., 2007; Potts et al., 2016; Rader et al., 2016). Insect pollinators are diverse and mostly represented by Coleoptera, Diptera, Lepidoptera and Hymenoptera, in particular bees (Rader et al., 2020; Requier et al., 2023; Wardhaugh, 2015). The diversity and abundance of insect pollinators are reported to decline globally due to multiple stressors such as environmental degradation, habitat loss, overuse of agrochemicals and climate change (Giannini et al., 2017; LeBuhn and Vargas Luna, 2021; Olynyk et al., 2021; Trunschke et al., 2024). Decline in the abundance and diversity of many wild pollinators (Ollerton, 2017; Zattara and Aizen, 2021), along with changes in their geographical ranges and phenology (Aguirre-Gutiérrez et al., 2016; Hegland et al., 2009; Martinet et al., 2015) are expected to increase pollination deficit, i.e. insufficient pollen reception (Garratt et al., 2021; Vaissière et al., 2011), and may become future limiting factors for agricultural production.

Climate change is known to disrupt plant-pollinator interactions through phenological mismatches, where plant flowering and pollinator activity become desynchronised (Settele et al., 2016). While some studies suggest that both plants and pollinators advance their activity with warming temperatures (Hegland et al., 2009), others indicate significant range contractions under extreme climate scenarios (e.g. SSP5–8.5) (Marshall et al., 2023). For instance, the populations of *Bombus terrestris* Linnaeus, 1758 (Hymenoptera: Apidae) are projected to lose habitat in southern Europe by 2100, despite potential expansions in northern regions (Marshall et al., 2023). These spatial and temporal shifts pose significant risks to agricultural productivity and food security. Although some evidence suggests that insects may be more resilient to climate impacts through behavioural adaptations (Holland and Bourke, 2015; Johnson et al., 2023), the extent to which climate change alters pollination services and crop productivity remains poorly understood.

Standardised field monitoring across Europe was conducted to assess the effects of temperature on pollinator communities and pollination services, using apple *Malus domestica* (Suckow) Borkh, 1803 (Rosaceae) orchards as a case study, to address this knowledge gap. Apples are the third most widely produced fruit globally (FAO, 2025) and require insect-mediated cross-pollination to enhance apple fruit set, seed set and fruit quality, such as apple size and weight (Pardo and Borges, 2020). Although managed honey bees *Apis mellifera* Linnaeus, 1758 (Hymenoptera: Apidae) are the most widely used pollinators of apples and many other crops, apple pollination relies on a diverse community of insects, including bumble bees, solitary bees and other non-bee pollinators such as flies, beetles and lepidopterans (Barahona-Segovia et al., 2023; Requier et al., 2023). However, pollination deficits occur in apple orchards and persist even with supplementation of managed honey bees (Garratt et al., 2014; Martins et al., 2015; Weekers et al., 2022). Flower visitors monitoring and pollination experiments were conducted in 33 sites across Mediterranean climates in four European countries and one North African country over two years (2022−2023) using standardised protocols. All study sites used the apple cultivar ‘Golden Delicious’. The analysis focused on how climate gradient (i.e. latitudinal temperature gradient) affects the abundance of flower visitors, pollination services and potential pollination deficits. To do so, the present work compared pollen deposition on flowers, apple fruit set, apple quality and yield among different pollination treatments (open pollination, open pollination + hand pollination and pollinator exclusion). Pollinator abundance was assessed using locally measured temperatures during flower visit observations (i.e. observation-time temperature) and WorldClim (https://www.worldclim.org/) long-term mean annual temperature data averaged over 1970–2000 (i.e. latitudinal temperature gradient). Pollination services were analysed using the latitudinal temperature gradient only. Lastly, the study estimated the economic value of apple pollination services and explored the potential impact of climate change on the economic outcomes of farmers.

This study aimed to determine: (i) how observation-time temperatures affect on the abundance of flower visitors, (ii) whether pollination services enhance fruit set and improve fruit quality for the benefits of the economic outcomes of farmers and (iii) how latitudinal temperature gradient affect both pollinators and pollination services. Addressing these questions provides critical insights for policymakers and agricultural stakeholders to develop strategies that mitigate climate change impacts on pollinator-dependent crops, promote sustainable agricultural practices and strengthen food security in a changing climate.

2. Materials and methods

2.1. Study sites and climate gradient

This study was conducted over two consecutive years (2022–2023) across the Mediterranean region, covering four European countries (Croatia, Slovenia, France and Greece) and one North African country (Algeria). A total of 33 sites were selected (i.e. orchards) along a climate gradient from 9.1 °C to 17.8 °C (Fig. 1). The sites were spatially grouped within regions (i.e. three to six commercial apple orchards per region) and were selected independently of their farming practices. Sites were located at least 2 km apart (i.e. the average foraging distance of honey bees, Steffan-Dewenter and Kuhn, 2003) to ensure spatial independence. Focus was placed exclusively on ‘Golden Delicious’ orchards, a variety with partial self-incompatibility (Olhnuud et al., 2022; Schneider and Goldway, 2001). To define the latitudinal temperature gradient, mean annual air temperature (°C) for each orchard site was extracted from WorldClim Version 2 Beta (https://www.worldclim.org/), considering mean annual values for the period 1970–2000 to account for interannual climatic variability. This approach resulted in a single representative long-term mean annual temperature value for each site.

2.2. Monitoring of flower visitors

Standardised transects were performed in each study site to record the richness and abundance of apple flower-visiting insects twice per year during the peak bloom period of apple trees (i.e. from mid-April to beginning of May). All transects were done between 9:30 a.m. and 5:30 p.m., taking care to have similar weather conditions, e.g. days with a wind speed of less than 15 km/h, no rain and at a minimum temperature of 13 °C in clear skies. Each transect consisted of a 100-m linear walk within the apple orchard, with a duration of about 15 min. During the transects, insects visiting apple flowers were recorded within a 1-m-width boundary and classified based on 11 categories recognised as insect pollinators in agriculture (Rader et al., 2020; Requier et al., 2023): (i) honey bees, (ii) bumble bees (*Bombus* spp.), (iii) other wild bees, (iv) wasps and hornets, (v) hoverflies (Syrphidae), (vi) other Diptera, (vii) butterflies (Lepidoptera), (viii) beetles (Coleoptera), (ix) ants (Hymenoptera), (x) hemipterans and (xi) other visitors. The observation-time temperature was recorded using a portable anemo-thermo-hygrometer device (Skywatch Atmos). The temperature value was registered after a period of 5 min for acclimation. A total of 65 transects within apple orchards across the 21 sites were performed.

2.3. Pollination treatments

Five apple trees were selected at each study site (i.e. orchard), ensuring a minimum spacing of 10 m between trees. A total of 272 trees were used during both years of experiments. Before flowering, one branch from each tree was arbitrarily selected. Three inflorescences at the balloon stage (before the flower blooms; Ackerman and Samach, 2015) on the branch were randomly assigned a pollination treatment, following the standardised FAO protocol (Vaissière et al., 2011): (i) open pollination (O) in which insects are free to visit the flower, (ii) open pollination + hand pollination (OH) and (iii) pollinator-excluded (E) in which insects are not able to visit the flower. The E inflorescences were left covered with a mesh bag (0·8 × 0·8 mm mesh) until petal abscission. To test pollen limitation, pollen supplementation protocols (OH treatment) (Ashman et al., 2004; Bierzychudek, 1981) was included. For that, pollen was collected from appropriate cross-pollinating cultivars on the day of the experiment and used a fine paintbrush to transfer it to the stigmas of opened flowers. Hand pollination was performed once during the blooming period. The number of buds on each inflorescence was used as the initial flower count.

2.4. Pollen deposition and pollen germination on stigmas

Flower styles were collected in 2023 for three pollination treatments (E, O and OH) in each study site. Styles were excised from flowers once their stigmas were no longer receptive to pollen and stored in a 70% ethanol solution at 4 °C until analysis. Stigmas were washed in deionised water, softened in 8 M NaOH for 16 h, and then thoroughly rinsed with deionised water prior to analysis. They were subsequently stained with an aniline blue solution (0.1% [*w/v*] in K_3PO_4, 0.1 M) for 24 h and

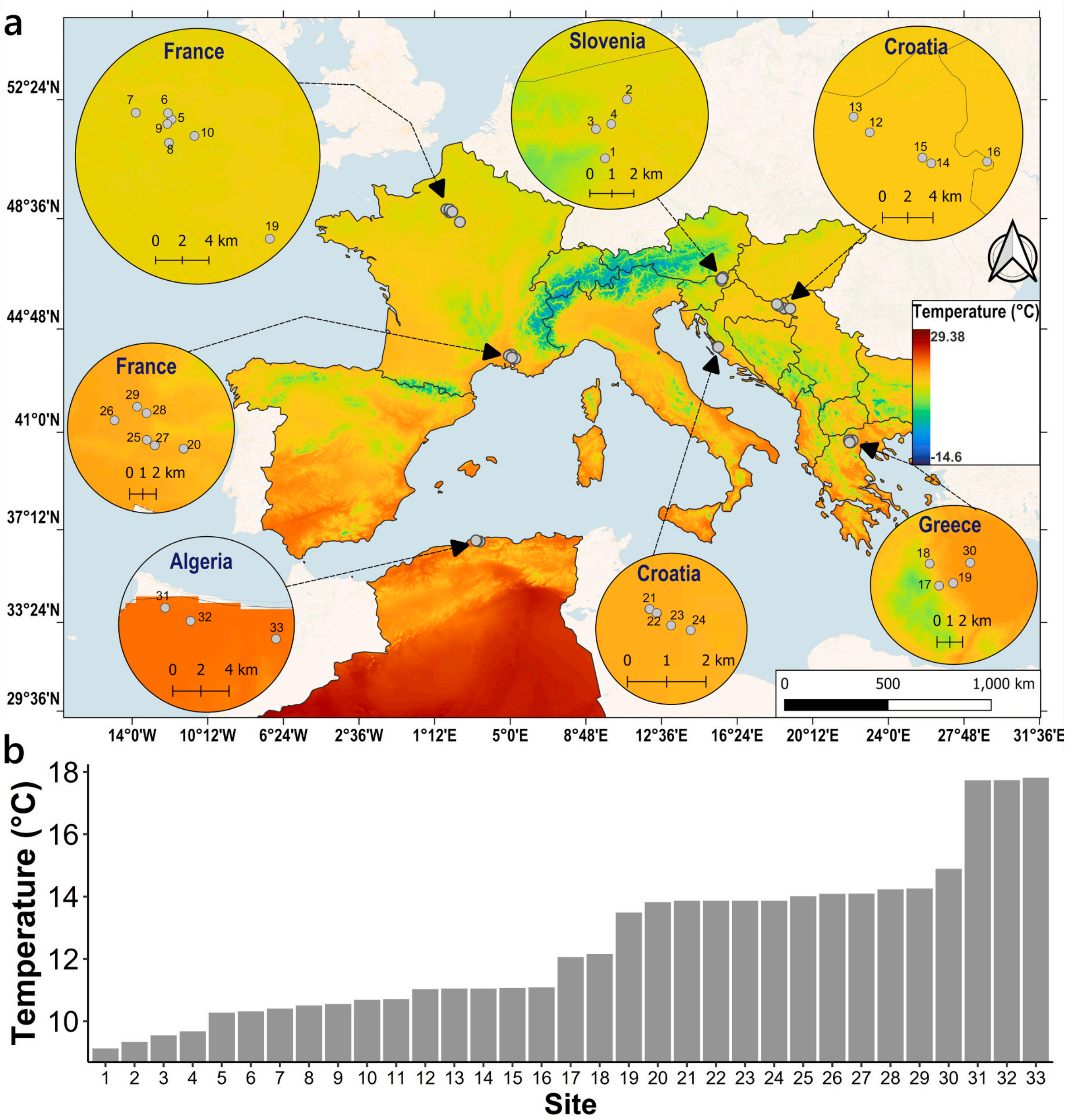

Fig. 1. a) Location of the 33 study sites across Europe. Each grey dot represents a study site (i.e. an apple orchard) and its associated number, ranked from coolest to warmest. The background colour gradient is the latitudinal temperature gradient for SSP126 (Shared Socioeconomic Pathway 1–2.6) 2011–2040. b) is the temperature in degrees Celsius at the site location based WorldClim mean annual temperature data averaged over 1970–2000 (**Error! Hyperlink reference not valid.**).

mounted on microscope slides following the protocol described by Martin (1959). Fluorescent microscopy was performed using a Leica DM6000B microscope, and images were acquired at 50× magnification using the LAS V4.5 software (Leica Microsystems Ltd.,Switzerland). For each sample, the number of pollen grains germinated on two stigmas per flower was counted using the ImageJ CellCounter plugin (Schneider et al., 2012).

2.5. Fruit set and fruit quality

In each study site and for each pollination treatment (E, O and OH), at least six weeks after bagging and before any thinning, the number of green fruitlets was counted to assess the initial fruit set. Final fruit set was determined in September before the commercial harvest, and ripe apples from each treatment were collected for further analysis. Apples were kept in a refrigerator and analysed within eight days. Fruit quality measures included fresh weight, maximum and minimum height and width using callipers and the number of developed seeds. Height symmetry was defined as the maximum minus the minimum height. The sugar concentration of each apple, expressed in units of °Brix, was determined using a hand-held optical refractometer.

2.6. Economic value

The contribution of pollinators to fruit set was calculated by subtracting the predicted final fruit success rate under pollinator exclusion from that observed under open pollination. This value was converted into the number of fruits per hectare using the following assumptions: each inflorescence produces five flowers (Eccher et al., 2014), each tree has 100 inflorescences and one hectare contains 500 apple trees. Thus, the equation for the number of additional fruits per hectare due to pollinators was:

$$No.of\ fruits/hectare = (\%final_O - \%final_E) \times 5 \times 100 \times 500 \quad (1)$$

The contribution of pollinators to apple yield was estimated by calculating the difference between the product of predicted apple weight and final fruit set under open pollination and the corresponding product under pollinator exclusion. (Eq. 2).

$$Pollinator - mediated\ apple\ yield\ (g) = (apple\ weight_O \times \%final_O) - (apple\ weight_E \times \%final_E) \quad (2)$$

The total economic value of pollination services was estimated using (Eq. 3). Apple yield from (Eq. 2) converted in kg per hectare was multiplied by €0.96 per kg, based on the average market price of apples. This value corresponds to the average producer price for dessert apples in the European Union in 2022–2023 (European commission, 2023).

$$\text{Economic value } (€/\text{ha}) = \text{Pollination services to apple yield} \times 5 \times 100 \times 500/1000 \times 0.96 \quad (3)$$

Changes in economic value across a temperature gradient were quantified to evaluate the economic impact of climate change on pollination services. Specifically, the difference in yield and monetary value between a reference temperature was estimated, where pollination services were highest and at high temperatures. This approach allowed us to assess how warming influences pollination-mediated apple yield and revenue.

2.7. Statistical analysis

All data were analysed in R, version 4.2.3 (R Core Team, 2024). A series of generalised linear mixed models (GLMMs) were fitted using the glmmTMB R-package (Brooks et al., 2017) to analyse response variables spanning flower visitor abundance, pollen germination, fruit and seed set and fruit quality traits. All models included treatment, long-term mean annual temperature (i.e. latitudinal temperature gradient), year and their interactions as fixed effects. The flower visitor abundance model also included the observation-time temperature, visitor morphogroups and their interactions as fixed effects. The random structure of all models accounted for the nested sampling design, with plot nested within site and site within region (and where relevant inflorescence identity within plots). Count data (i.e. flower visitor abundance, seed set, fruit symmetry) were modelled with Poisson or negative binomial distributions, proportions (i.e. initial and final fruit set) with a binomial distribution with a logit link and continuous traits (fruit weight and sugar content) with a Gaussian distribution. Additionally, a linear model with year, latitude and their interaction as explanatory variables was fitted using the dates of flower-visitor observations—used as a proxy for flowering time—to assess potential latitudinal effects on apple blooming time. Post-hoc multiple comparisons were conducted using the Holm adjustment in the *emmeans* R package (Lenth, 2024) R-package to assess differences between pollination treatments. Model fits were visually assessed using QQ plots and tested for overdispersion with the *testDispersion* function in the *DHARMa* R-package (Hartig, 2021). Model predictions were generated using the *ggpredict* function from the *ggeffects* R-package (Lüdecke, 2018), and statistical significance of model parameters was determined using Type III ANOVA (*car* R-package). Results were reported as chi-square (χ^2) and p values, considering a threshold of 5% for significance. The climate impact on the economic outcomes of farmers was evaluated by first using model predictions of fruit set and apple weights to calculate apple yield and the associated economic outcomes (see above). Model predictions of the effects of pollination treatment and long-term mean annual temperature were then used to estimate the relative contribution of climate to pollination services (see above).

3. Results

3.1. Temperature effect on flower visitors

Flower visitor abundance was significantly influenced by visitor species, observation-time temperature, year and the interaction between visitor species and observation-time temperature (Table S1). In 2023, flower visitor abundance was 8.8% higher than in 2022 (coefficient = 0.08481, $\chi^2 = 5.91$, df = 1, $p = 0.015$). Honey bees were the dominant flower visitors, and they significantly differed from all other species (Fig. 2a). Warm temperatures increased honey bee visitation but had a

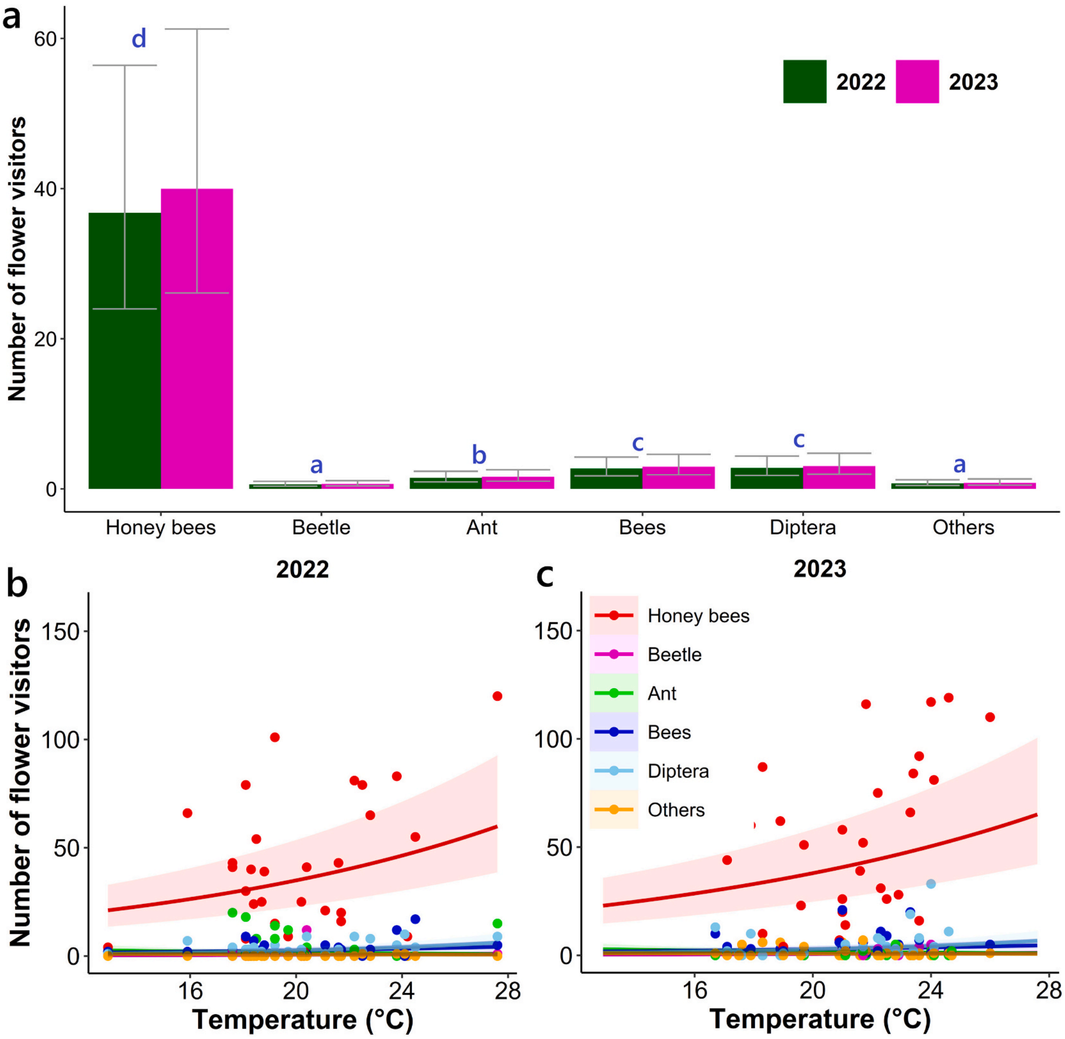

Fig. 2. An analysis of the abundance of flower visitors predictions based on GLMM. a) Predicted apple flower visitor abundance. Different colours show different years and the letters in blue show the pairwise comparison significance. b and c are similar predictions against observation-time temperature values. Different colours in b and c represent different morphogroup types. Coloured dots are the observed values of flower visitors. Thick lines show the GLMM predictions with shaded areas indicating the 95% CI.

weak effect on other flower visitor morphogroups in both years (Fig. 2b & c). Flowering time increased significantly with latitude (≈1.8 days per degree; $F = 201.98$, $df = 1$; $p < 0.001$), while the year × latitude interaction was not significant ($F = 2.71$, $df = 1$, $p = 0.10$), indicating a consistent latitudinal gradient across years (Fig. S1).

3.2. *Climate effect on pollen germination, fruit set and fruit quality*

The number of germinated pollen grains deposited in apple flowers was significantly affected by pollination treatment, with fewer germinated pollen grains when pollinators were excluded compared to pollinator-involved treatments (Table S2a & Fig. 3a). However, hand-pollination supplementation did not significantly increase pollen germination (Fig. 3a). For the fruit set, initial fruit formation was significantly affected by pollination treatment and year (Table S2b & Fig. 3b). At the same time, the final fruit set was influenced by pollination treatment, year, long-term mean annual temperature and the interaction between pollination treatment and long-term mean annual temperature (Table S2c, Fig. 3c & Fig. 3d). Similar to germinated pollen grains, both initial and final fruit set success were lower when pollinator visitation was excluded. Warm site temperatures consistently increased the final fruit set in O and OH pollination treatments, while the E treatment showed a curvilinear response (Fig. 3d).

Apple quality was assessed based on seed number, fruit weight, symmetry and sugar content. Seed numbers were significantly affected by pollination treatment and year (Table S3a), while fruit weight was affected by pollination treatment, year and the interaction between treatment and temperature (Fig. 4c & Table S3b). Apple symmetry was primarily driven by year, with a significant interaction between pollination treatment and temperature ($\chi^2 = 6.04$, $df = 2$, $p = 0.0485$; Table S3c & Fig. S2). Sugar content was significantly affected by year and temperature, but not by pollination treatment (Table S3d). The contribution of pollinators to apple symmetry increased with rising temperatures (Fig. S3a). Sugar content increased with temperature across all treatments (E, O and OH) suggesting a positive relationship between temperature and apple sugar concentration, independent of pollination effects (Fig. S3b & c). Post-hoc analysis revealed that excluding pollinators (E) resulted in significantly different seed numbers compared to O and OH, and significantly different apple weights compared to O (Fig. 4a & b).

3.3. *Climate effect on pollinator-mediated apple yield and economic value*

The final fruit set from O treatment increased along the climatic long-term mean annual temperature in a linear pattern, while the final fruit set from E treatment surprisingly increased following a curvilinear

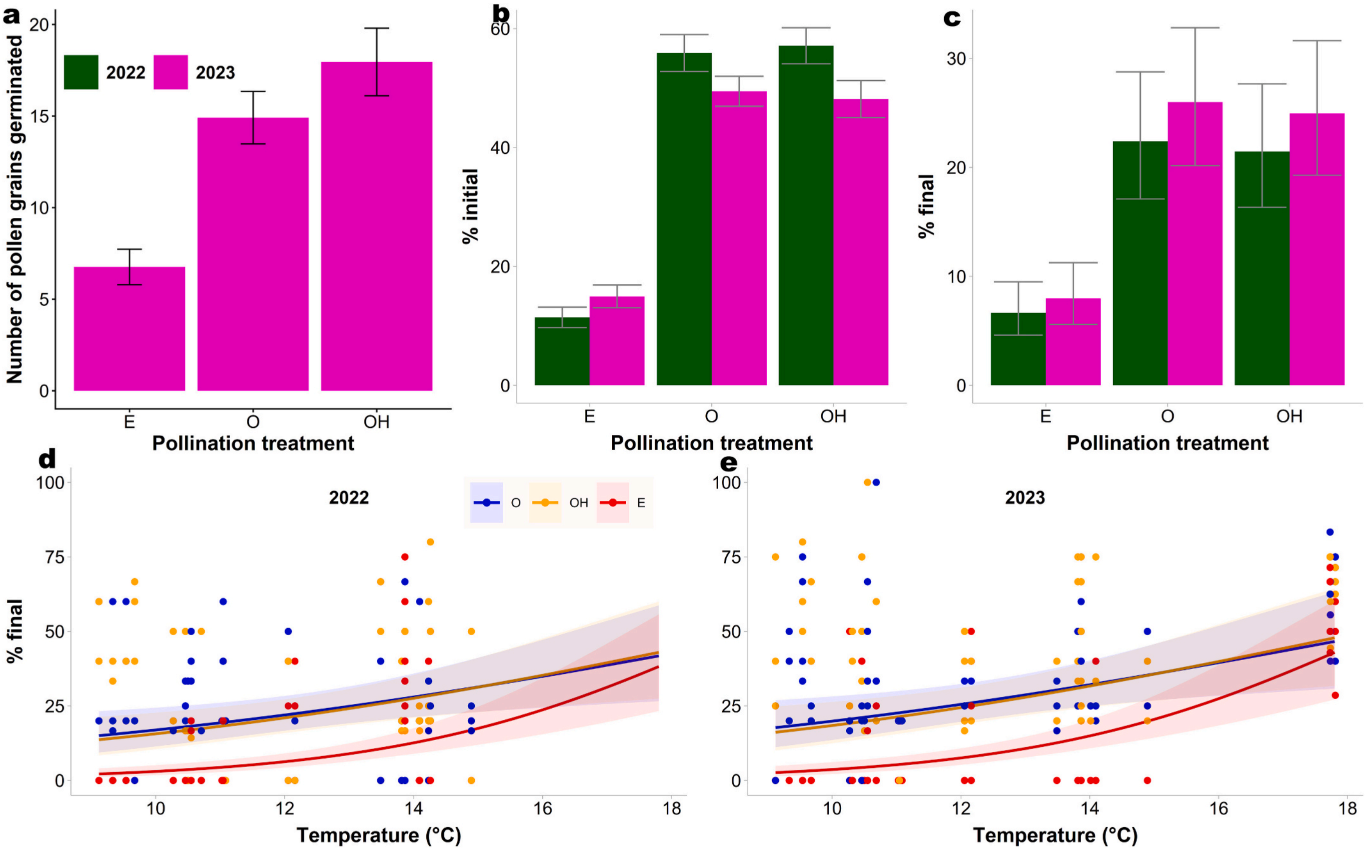

Fig. 3. a) Observed number of germinated pollens b) observed success rate of initial fruits, c) predicted success rate of final fruit set based on GLMM, Different colours in b and c are different years. The letters within the bar plot indicate the results of pairwise comparisons between treatments. d) Effects of long-term mean annual temperature on the predicted final fruit set percentage per treatment. Different colours show different treatments. Thick lines indicate GLMM predictions, with shaded areas representing 95% confidence intervals.

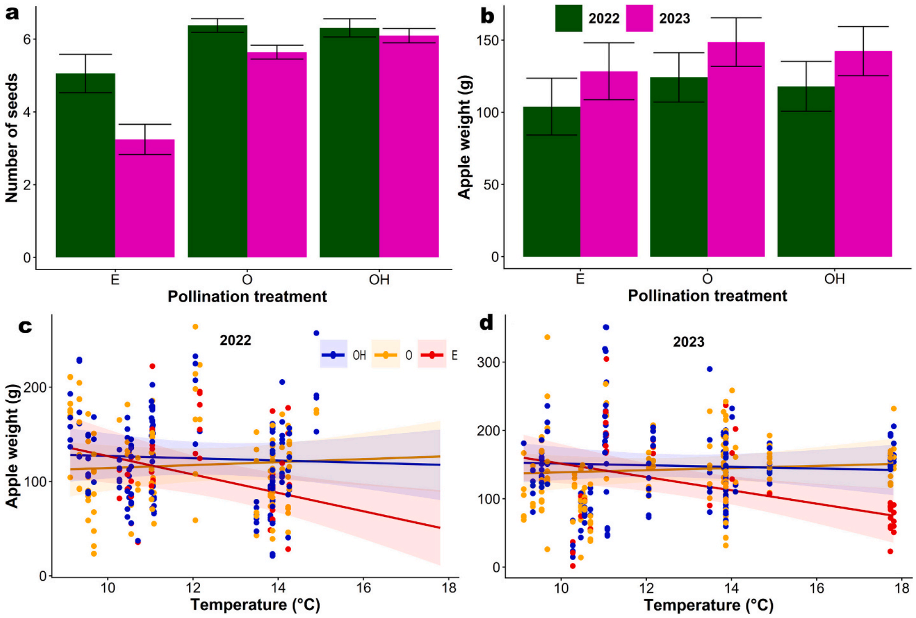

Fig. 4. Analysis of apple fruit quality based on GLMM predictions. a) Bar plots showing the observed seed numbers and b) bar plots showing the predicted apple weights. Different colours show different years while the letters above the bar plots show the pairwise comparison. c) Effects of long-term mean annual temperature on the predicted apple weight per treatment. Different colours show different treatments. Thick lines indicate GLMM predictions, with shaded areas representing 95% confidence intervals.

response (Fig. 3d, e and S4a). As a result, the contribution of pollinator-mediated pollination to final fruit set (quantified as the difference between open-pollinated and pollinator-excluded treatments) followed a unimodal response along the long-term mean annual temperature in both years (Fig. S4c). Although apple weight declined with temperature in both the O and E treatments, the decline was steeper under pollinator exclusion (Fig. S4b). As a result, the contribution of animal-mediated pollination to apple weight increased with the temperature for both years (Fig. S4d).

Although the animal-mediated pollination decreased along the long-term mean annual temperature gradient, apple yield increased linearly for both years (Fig. S4e), by approximately 82% in 2022 (from 16.3 to 29.7 g) and by 49% in 2023 (from 22.8 to 33.9 g). In economic terms, this yield increase translates to benefits for farmers from €3911 to €8139 per hectare in 2022 and from €5472 to €7137 per hectare in 2023 (Fig. S4f).

4. Discussion

This study provides important insights into how pollination services and temperature jointly influence apple productivity across a latitudinal temperature gradient in Europe and Northern Africa. Both observation-time temperature and latitudinal temperature gradient, along with flower visitor abundance and their interactions, significantly affect key apple production metrics, including fruit set, fruit quality and its economic value.

Apple cultivars are partially self-incompatible, relying on insect-mediated cross-pollination to maximise yields and fruit quality (Olhnuud et al., 2022). Managed honey bee supplementation has become a common practice to mitigate pollination deficits (Rollin and Garibaldi, 2019). However, wild bee communities play a vital role in providing pollination services, particularly under fluctuating climatic conditions (Weissmann et al., 2021). Studies have shown that wild pollinators can extend the range of active pollination, even under adverse weather conditions such as high wind speeds (Brittain et al., 2013). Burns and Stanley (2022) found that hoverflies frequently visited Irish orchards, while solitary bees carried substantial amounts of pollen despite their low abundance. Similarly, Garratt et al. (2016) estimated that wild bees contribute approximately €51.4 million annually to apple pollination in the UK, compared to €21.4 million from honey bees. In the present study, honey bees were the dominant pollinators, with an 8.8% increase in visitation rates in 2023 compared to 2022. This dominance aligns with previous research demonstrating the widespread presence of honey bees in apple orchards (Bernauer et al., 2022; Geier et al., 2024; Ramírez and Davenport, 2013). Honey bee visitation rates increased significantly with observation-time temperature, aligning with research showing their activity positively correlates with warm conditions (Jhawar et al., 2023; O'Connell et al., 2024). Although other pollinators were less abundant in this study, promoting wild pollinator populations could serve as a viable alternative to reducing reliance on managed honey bees (Garibaldi et al., 2017).

The importance of pollinators was further underscored by the significant differences in pollen germination and fruit set between pollinator-excluded and open-pollinated treatments. The exclusion of pollinators resulted in markedly lower pollen germination rates, initial fruit set and final fruit set, highlighting the indispensable role of animal pollination. The contribution of animal-mediated pollination to final fruit set declined with an increase in temperature, suggesting that rising temperatures reduce the benefits of pollinators for apple fruit production. Comparable findings have been reported globally. For instance, Geslin et al. (2017) observed that high-quality honey bee management increased fruit set by 15% and the profits of farmers by 70% in Argentina. Similarly, Park et al. (2016) reported that honey bees contributed more to pollination in Nova Scotia compared to other pollinators due to their great relative abundance, even though per-visit efficiency was similar across species.

The surprising effect of rising temperature on the pollinator-exclusion treatments (i.e. the E treatment) suggest that a process other than animal-mediated pollination may be at play. It can be hypothesised that self-compatibility increases with temperature, as observed in the *Citrus* × *clementina* hort. ex Tanaka (Rutaceae) (Aloisi et al., 2020). Another hypothesis would be wind-mediated pollination. In our study, the pollinator-excluded treatment did not exclude the wind, and it is known that wind occurs more intensively in Mediterranean regions than in other colder European regions (Fei et al., 2023). Based on field observations, some Mediterranean sites had specialized orchard management practices that could potentially benefit from wind-mediated pollination. For example, farmers in Algeria had a habit of checking and fixing freshly cut pollinizer branches (i.e. branches from pollen donor trees) across their orchards (Yamina Haider, pers. obs.). The hypothesis behind this management strategy is that the frequent winds in these Mediterranean sites may facilitate apple pollination. In further study, the use of bags allowing the exclusion of anemophilous pollination could help the understanding of the observed results along the long-term mean annual temperature. Moreover, as this study is correlative rather than causal, future experimental research is encouraged to investigate these potential mechanisms and determine whether temperature affects pollinator limitation or improved self-compatibility. While this study did not explicitly compare the effectiveness of honey bees versus other species, the present results align with extensive evidence highlighting the critical role of pollinators in boosting apple fruit set.

Fruit quality, as assessed by seed number, apple weight, symmetry and sugar content, was strongly influenced by both pollination and temperature. Pollinator-involved treatments consistently produced apples with higher seed numbers and greater weight compared to pollinator exclusion. This was also reported in Bhutan where Dorji et al. (2022) found out that high abundance of flying insects increased apple quality in terms of seed number, weight and sugar content. Under warm conditions, apples from pollinator-involved treatments were noticeably heavier than those from pollinator-excluded treatments. Similar trends of positive influence of rinsing temperature on apple quality have already been reported (Lee et al., 2023a; Warrington et al., 1999). However, temperature elevation has also been associated with decreased shoot growth and leaf photosynthetic rate, with possible impairment to fruit quality (Lee et al., 2023b). In this study, warming conditions increased apple sugar content regardless of pollination treatments. For apple symmetry and weight, the contribution of animal pollination increased with an increase in temperature. Given the overwhelming abundance of honey bees in our study, these conclusions primarily apply to honey bee mediated pollination of apples. This suggests that future apple productivity may rely heavily on managed honey bees. The potential ecological consequences of high-density managed honey bees (Magrach et al., 2025; Travis et al., 2025) also call for conservation efforts that promote wild pollinator populations.

From an economic perspective, apple yield increased along the climatic long-term mean annual temperature, although animal-mediated pollination decreased. In Ireland, insect pollination was found to contribute 93% to Jonagored apples and 46% to the Dabinett cultivar (Burns and Stanley, 2022). A global meta-analysis by Olhnuud et al. (2022) showed that, relative to pollinator-excluded flowers, apple fruit set and seed set increased by 71% and 62% when insects had open access. In Argentine Patagonia, Hünicken et al. (2021) reported that pollinator exclusion reduced apple fruit set by 71–92%. These results highlight the significant economic value of pollination services, particularly in light of climate change projections. This study highlights the vital role of pollinators in maintaining agricultural productivity and underscores how temperature changes influence pollination dynamics.

Beyond pollination deficits, climate change introduces additional challenges for crop production, such as inadequate winter chilling (Delgado et al., 2021) and suboptimal post-bloom temperatures (Tromp and Borsboom, 1996). As global temperatures rise, ensuring healthy pollinator populations will be essential for securing both crop yields and economic value. To protect pollination services and support sustainable apple production, targeted conservation efforts such as preserving habitats and adopting climate-resilient farming practices, are necessary. These strategies will be crucial for safeguarding food production in the face of a changing climate.

While this study provides important insights into how temperature affects pollination services and apple productivity, there were several limitations. Although data collection was standardised across sites and years, key local environmental factors such as humidity, wind speed and solar radiation were not included in the models, despite their known influence on pollinator activity. Honey bees were the dominant flower visitors, but pollinator efficiency was not assessed, so the relative contributions of different insect groups remain unclear. The study focused on a single cultivar ('Golden Delicious'), which enabled consistent comparisons across regions, but this limits the applicability of the findings to other apple varieties with different climatic sensitivities or pollination requirements. Although the models revealed significant and robust effects of pollination and climatic variables, future studies could benefit from incorporating additional site-level variables, such as the number and location of managed pollinators (e.g. honey bee hives) within a 3 km radius of the orchards. Considering managed pollinator metrics as additional explanatory variables may help to explain the remaining variance in the models. Future studies could also consider possible variations in thinning management practices. The economic estimates, though derived from experimental data, relied on simplified assumptions such as fixed market prices, uniform management practices and no production costs, which may not reflect real-world variability. Lastly, temperature was the only climatic factor considered. Future work should integrate additional stressors, such as insufficient winter chilling, rainfall variability and extreme weather events, to better capture the multiple climate-driven pressures affecting pollination services and crop performance. Addressing these limitations will be key to refining predictive models and supporting the development of more targeted, climate-resilient agricultural strategies.

5. Conclusion

This study highlights the dependence of apple production on climate and underscores the influence of temperature on pollination services. The present study shows that warm observation time temperatures enhance pollinator activity, particularly the abundance of honey bees. Warm latitudinal temperature gradients increase the yield and the economic benefits increase, but the animal-mediated pollination decreases with temperature. Given the correlative nature of this study, it cannot be determined whether temperature-driven changes in yield result from increased pollinator limitation, increased wind-mediated pollination, improved self-compatibility or a combination of all these processes. Future experimental studies are needed to disentangle these mechanisms and test the effects of temperature on pollinator activity, pollinator limitation and plant reproductive traits. Such work will be essential to better anticipate how ongoing climate warming may shape pollination services and apple productivity, and to inform adaptive, climate-resilient agricultural strategies.

CRediT authorship contribution statement

Clémence Riva: Writing – original draft, Methodology, Investigation, Data curation. **Stella Gachoki:** Writing – review & editing, Writing – original draft, Validation, Investigation, Formal analysis, Data curation. **Noureddine Adjlane:** Resources, Funding acquisition. **Danilo Bevk:** Validation, Resources, Investigation, Funding acquisition. **Yamina Haider:** Investigation. **Fani Hatjina:** Validation, Resources, Funding acquisition. **Šimun Kolega:** Validation, Resources, Investigation. **Marin Kovačić:** Investigation. **Ioannis Manthos:** Investigation. **Zlatko Puškadija:** Investigation. **Thomas Sotiropoulos:** Investigation. **Bojan Stipešević:** Validation, Resources, Investigation, Funding acquisition. **Fabrice Requier:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2026.181767.

Data availability

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.19403906

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