Short Communication

ASSESSING POLLINATOR EFFICIENCY IN BLUEBERRY: FROM BUMBLEBEE BUZZING TO ANT FORAGING

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Abstract—Highbush blueberry (*Vaccinium corymbosum*) depends on biotic pollination to produce marketable fruits. A wide range of insects, from managed honey bees (*Apis mellifera*) to wild bees, hoverflies and other insects, visit blueberry flowers, but their efficiency as pollinators varies greatly. This variation is partially related to blueberry flower morphology, which limits access to nectar and pollen, and to the presence of poricidal anthers that require buzz pollination for more efficient pollen release.

We assessed the pollination efficiency of the main floral visitors of blueberry in Portugal. Previously bagged flowers of cultivar Duke were exposed to individual visitors, and pollen loads on stigmas were quantified after each visit. Additionally, we monitored plant-pollinator interactions throughout the day and assessed pollen deposition on the stigmas from flowers exposed to open pollination.

Surprisingly, most visits were made by the ant *Formica rufibarbis*, closely followed by the bumblebee *Bombus terrestris*. These were also the only taxa recorded visiting flowers within the pollinator efficiency experiment. *Bombus terrestris* deposited significantly more pollen tetrads, and flowers visited by this species consequently developed more pollen tubes than those visited by *F. rufibarbis*. However, open pollinated flowers exhibited greater pollen deposition and higher pollen tube numbers than flowers visited by either *B. terrestris* or *F. rufibarbis*. Our results indicate that *B. terrestris* is a more efficient pollinator than *F. rufibarbis* and can deliver sufficient pollen tetrads to achieve full pollination in a single visit, depending on its foraging behaviour. Despite their low efficiency, ants may still contribute to blueberry pollination under conditions that limit the activity of flying pollinators.

Keywords—*Bombus terrestris*; *Formica rufibarbis*; Non-bee pollinators; Pollination; Pollen loads; *Vaccinium*

INTRODUCTION

In highbush blueberry (*Vaccinium corymbosum*), both yield and fruit quality strongly depend on biotic pollination (as reviewed by DeVetter et al. 2022). In commercial orchards, the main pollinators are often managed species such as *Apis mellifera*. Still, a wide range of wild bees, including *Bombus* spp. and solitary bees of the genera *Lasioglossum*, *Anthophora*, *Osmia* and *Andrena*, also visit blueberry flowers and act as effective pollinators (Eeraerts et al. 2019, 2023; Castro et al. 2023). Non-bee pollinators are thought to be uncommon, likely due to the flower's morphology, which limits access to nectar and pollen (Isaacs & Kirk 2010; Cavigliasso et al. 2021). Blueberry nectar is produced at the base of the corolla, and the small, urn-shaped, downward-facing flowers restrict access to floral rewards, thereby influencing both pollination efficiency and visitor behaviour (Borghi et al. 2025). Moreover, blueberry anthers are poricidal and release pollen most effectively under buzz pollination (Vander Kloet 1988). Consequently, not all floral visitors are equally efficient pollinators, and fruit set and weight can vary greatly depending on the taxon of the visiting insect (Cortés-Rivas et al. 2023b). For example, bumblebees (*Bombus* spp.) have been

shown to be more efficient pollinators of blueberry than honey bees (*Apis mellifera*), likely due to their ability to buzz-pollinate and their higher per-visit pollen deposition (Sun et al. 2021; Eeraerts et al. 2023). Bumblebees have also been reported to deposit a higher number of pollen tetrads (groups of four fused pollen grains, typically released by *Vaccinium*) on stigmas compared to honey bees, syrphids and certain solitary bees (Bobiwash et al. 2018; Cortés-Rivas et al. 2023b). Highbush blueberry flowers have, on average, around 100 ovules, and each ovule requires one to five pollen tubes for successful fertilization (Komatz et al. 2025). Each pollen tetrad can grow one to four pollen tubes, and between 30 to 100 tetrads are needed to maximize fruit set and weight (Dogterom et al. 2000; DeVetter et al. 2022), although as much as 125 tetrads have been suggested for optimal yield (Dogterom et al. 2000; Ramírez-Mejía et al. 2024a, 2024b). Identifying which flower visitors are the most efficient pollinators is thus essential to improve management practices impacting pollination success. In this study, we aimed to assess the pollination efficiency of the main visitors to the blueberry cultivar Duke by quantifying pollen deposition on stigmas following visits by different taxa.

MATERIALS AND METHODS

STUDY SITE

The study was conducted using northern highbush blueberry plants of the cultivar Duke grown in an experimental orchard at the Agrarian Field Station of Viseu, central Portugal (40°39'52.4"N, 7°54'12.6"W). The orchard comprised 20 cultivars and was originally established to assess the suitability of different blueberry cultivars for cultivation and production under the regional climatic conditions. Plants were grown directly in the soil in east-west-oriented rows, with each cultivar represented by 15-18 plants within a single row. The orchard was embedded in a heterogeneous landscape comprising multiple land-cover and land-use types, including mixed fruit orchards, grasslands, forests and urban areas, representative of agricultural landscapes commonly found in Portugal. No managed honey bee hives were introduced into the orchard during the study period.

POLLINATOR COMMUNITY AND EFFICIENCY

The floral visitor community was characterized following standard methodologies (Dafni et al. 2005). Briefly, flowering plants of cultivar Duke were observed for 5-minute periods at different times throughout the day, between 9:00 and 17:00 (CET+1), on four days distributed across the flowering period (April 7th to April 28th, 2025), resulting in a total of 35 monitoring periods. Observations were conducted only under weather conditions suitable for pollinator activity (i.e., sunny conditions with temperature above 13 ºC). During April 2025, the mean minimum and maximum temperatures were 8.2 ºC and 17.7 ºC, respectively, and cumulative precipitation was 134.9 mm (Table S1). During each observation period, we recorded the number and identity of the insects visiting the flowers, the number of flowers visited per insect, and the total number of open flowers. Floral visitors were identified using photographs and, when necessary, targeted captures, with identifications subsequently verified by expert entomologists. Visitation rates per taxon (%) were calculated as: Visitation rates (%) = (total number of flowers visited per plant, taxon and monitoring moment / number of flowers open per plant and monitoring moment) × 100.

To assess pollinator efficiency, we randomly marked 18 inflorescences across 10 individual plants. Each inflorescence was excluded from pollinators by covering them with fine tulle bags prior to bloom. Once the flowers opened, inflorescences were unbagged individually and observed for 10 minutes. Immediately after a floral visit, the flowers were labelled with the identity of the visitor, the inflorescence rebagged, and the pistils collected 48 h later in 70% ethanol for subsequent quantification of pollen loads and pollen tube development. Inflorescences remained bagged when not under observation. Although collection 72 h after pollination would have been ideal, this was not feasible due to logistical constraints and adverse weather forecasts; however, the 48h interval was sufficient to allow assessment of pollen tube growth. Additionally, pistils were also randomly collected from open pollinated flowers to quantify the natural pollination. To ensure that all samples from open pollinated flowers were collected at a comparable developmental stage and were exposed to floral

visitors for most of the flower's functional lifespan, we selected flowers that had already shed their corollas, but whose pistils had not yet begun to senesce, as indicated by browning.

Pollen loads and pollen tube observations

Pistils, 14 from flowers visited by *F. rufibarbis*, 15 from flowers visited by *B. terrestris*, and 20 from open pollinated flowers, were stained with aniline blue and observed under fluorescence microscopy following a protocol adapted from Dafni et al. (2005). Briefly, pistils were softened in 8M sodium hydroxide for 2 h at room temperature. The pistils were then rinsed in 96% ethanol, stained with aniline blue overnight, and carefully squashed on glass slides for observation under a fluorescence microscope (Leica DM 4000b; magnification 200×). Pollen tetrads were clearly visible and easily distinguishable, and their numbers were quantified by direct counting. Pollen tubes were counted at the midpoint of the style.

Data analysis

All statistical analyses were performed in R version 4.3.0 (Core Development Team 2016). To test the effect of visitor identity on the number of pollen grains and pollen tubes, we fitted linear mixed-effects models using the lmer function in the lme4 package (Bates et al. 2015). The response variables were the number of tetrads on the stigma and the number of pollen tubes counted at the midpoint of the style. Visitor identity was included as a fixed factor, and inflorescence as a random factor. Number of tetrads and pollen tube counts were square-root transformed prior to analysis to meet assumptions. Fixed effects were evaluated using analysis of variance (ANOVA). Post hoc pairwise comparisons were conducted using estimated marginal means with Tukey-adjusted *P* values (emmeans package; Lenth & Piaskowski 2026). Statistical significance was set at $P < 0.05$. Model fit was assessed using diagnostic plots from the DHARMa package (Hartig 2016). All figures were produced using ggplot2 (Wickham et al. 2024). Plots are presented using the original, untransformed values.

Results and Discussion

Surprisingly, the main floral visitor of the blueberry cultivar Duke was the ant *Formica rufibarbis* (Fabricius, 1793), which accounted for 44.63% of all recorded visits, closely followed by the bumblebee *Bombus terrestris* (Linnaeus, 1758; 41.81%). Other visitors were comparatively rare, representing minor proportions of total visits and included: *Anthophora plumipes* (Pallas, 1772; 6.82%), *Osmia bicornis* (Linnaeus, 1758; 2.70%), *Xylocopa violacea* (Linnaeus, 1758; 1.21%), *Lasioglossum* spp. (2.02%) and *Eucera* sp. (0.81%). However, *F. rufibarbis* and *B. terrestris* were the only species recorded visiting the flowers used in the pollinator efficiency experiment. This contrasts with observations made at the same site and cultivar in 2023, when the main pollinators of Duke were *B. terrestris* and *A. plumipes* (Castro et al. 2026). This difference may reflect interannual climatic variation, as temperatures were lower and rainfall substantially higher in 2025 compared to 2023 (Table S1), potentially affecting insect foraging activity and, consequently, the composition and relative abundance of floral visitors.

Bombus terrestris deposited significantly more pollen tetrads than *F. rufibarbis* ($X_2 = 125.0$; $P < 0.001$; Fig. 1A), which resulted in significantly more pollen tubes at the mid-style region of pistils ($X_2 = 136.7$; $P < 0.001$; Fig. 1B). These results indicate that *B. terrestris* is considerably more efficient than *F. rufibarbis* as a pollinator of blueberry flowers. On average, *B. terrestris* deposited 46.0 ± 8.75 (range: 0–117; estimated mean: 6.05 ± 0.90 and 95% CI: 4.15-7.95) pollen tetrads per visit, which grew on average 45.60 ± 5.17 (range: 18–89; estimated mean: 5.18 ± 0.80 and 95% CI: 3.51-6.85) pollen tubes. These values are comparable to those reported by Sun et al. (2021; 34.71) for the cultivar Bluecrop and by Cortés-Rivas et al. (2023a) for 'Duke' following visits without insect sonication, though lower than those obtained after visits in which sonication occurred.

Our findings suggest that a single visit by *B. terrestris* can fully pollinate a blueberry flower, considering that successful fertilization typically requires 30 to 100 pollen tetrads (Dogterom et al. 2000; DeVetter et al. 2022, Ramírez-Mejía et al. 2024b). However, pollen deposition likely depends on *B. terrestris'* foraging behaviour. Whether individuals are collecting pollen (with or without buzzing) or foraging for nectar can affect the amount of pollen they carry and, hence, the amount deposited on stigmas (Nunes-Silva et al. 2013; Cortés-Rivas et al. 2023a; Cortés-Rivas et al.

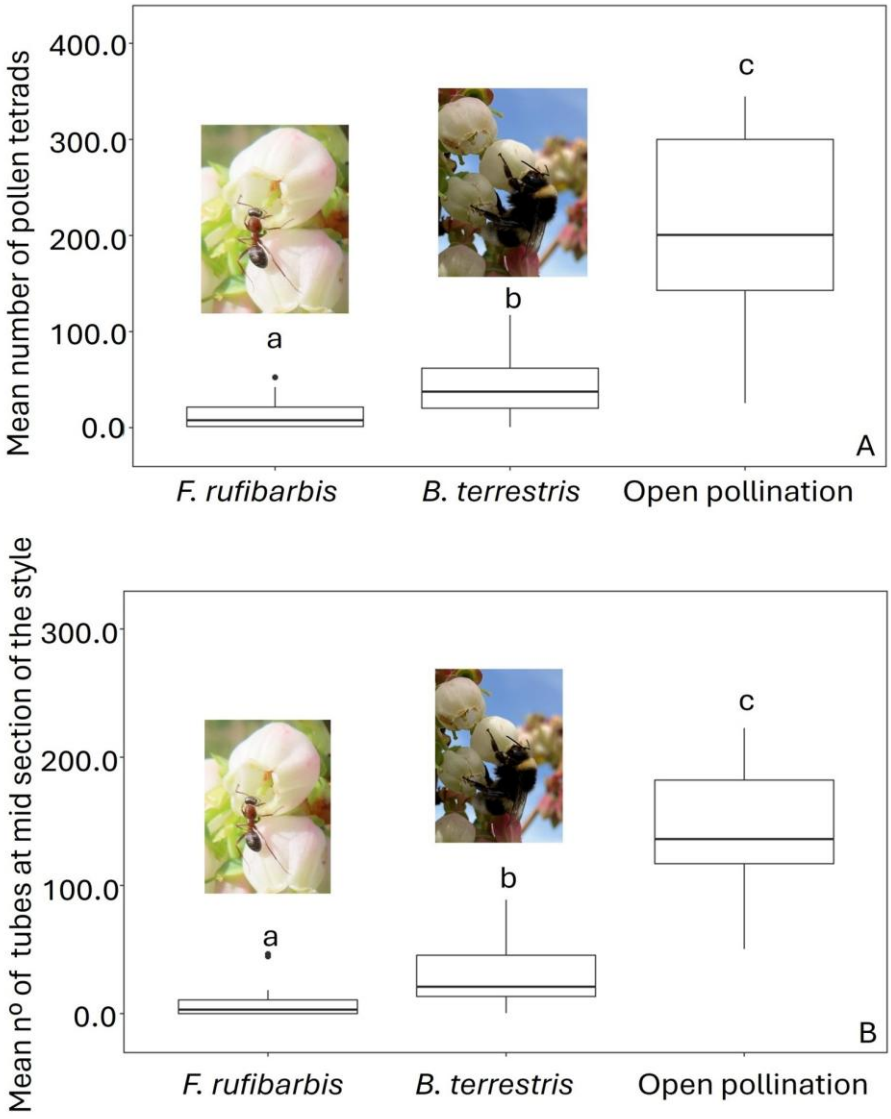


Figure 1. Number of pollen tetrads on the stigmas (A) and pollen tubes reaching the midpoint of the style (B) in flowers of highbush blueberry (*Vaccinium corymbosum* cv. Duke) exposed to visits by ants (*Formica rufibarbis*; *N* = 14), bumblebees (*Bombus terrestris*; *N* = 15), or open pollinated (N = 20) by the local pollinator community. Different letters indicate significant differences among cultivars at *P* < 0.05

2023b). Additionally, from a commercial perspective, fruit size is important. Blueberry fruit size is linearly related to the number of tetrads deposited up to a threshold between 112 (Ramírez-Mejía et al. 2024b) and 125 tetrads (Dogterom et al. 2000), with the number of tetrads required for optimal pollination varying between 112 and 274 (Ramírez-Mejía et al. 2024b). Results from open-pollinated flowers fall within this optimal range (210.35 ± 19.58 pollen tetrads per flower; estimated mean: 14.10 ± 0.71 and 95% CI: 12.63-15.57) and indicate that multiple visits by *B. terrestris* and/or complementarity by other pollinator species enhance pollen deposition. Enhanced pollen deposition is likely to translate into improved pollination outcomes, although these downstream variables were not measured in this study.

Formica rufibarbis deposited on average 14.50 ± 4.76 (range: 0–53; estimated mean: 2.93 ± 0.89 and 95% CI: 1.08-4.79) pollen tetrads, which produced 10.00 ± 4.76 (range: 0–47; estimated mean: 2.04 ± 0.79 and 95% CI: 0.39-3.68) pollen tubes. Although these numbers are low relative to optimal blueberry pollination requirements, they may still be sufficient for the flower to set fruit (Dogterom et al. 2000, Ramírez-Mejía et al. 2024b). As few as 10 tetrads can achieve approximately 70% fruit set in the cultivar Bluecrop, though the resulting fruits were smaller and contained fewer seeds (Dogterom et al., 2000), making them unsuitable for commercial purposes. Ants have been reported as pollinators in some crops, particularly those with small flowers, such as gooseberry (*Ribes rubrum* L.), raspberry (*Rubus idaeus* L.), and mango

(*Mangifera indica* L.), where flower morphology matches their body size and facilitates contact with reproductive organs (Carvalheiro et al. 2010; Díaz et al. 2025). Considering *F. rufibarbis*, pollen transport among flowers by has been reported for the Caryophyllaceae species *Scleranthus perennis* (Svensson 1985, 1986). Svensson (1985) observed carryover of pollen of *S. perennis* by *F. rufibarbis* to multiple flowers visited sequentially, with most grains deposited in the first few flowers, a mean distance of pollen transfer of 6.2 cm and 72 % of all transferences being within plants. While *F. rufibarbis* ants are mainly predacious and trophobiotic, with their diet being primarily composed of insects and aphid secretions, they also feed, to a lesser extent, from juices exuding from plants, including nectar (Seifert & Schultz 2009, Fürjes-Mikó et al. 2025). In our case, during the 5-minute observation periods, ants were observed moving around inside the flower for variable lengths of time, sometimes for the entire monitoring period, likely foraging for nectar and/or small prey. When the ants left the flower, they moved to a nearby flower, either entering the flower or remaining on its exterior, or moved to other parts of the plant such as leaves and twigs. Given the observed behaviour, their limited mobility and low pollen-carrying capacity, ants are more likely to promote self-pollination rather than cross-pollination. Blueberry is largely self-compatible, so self-pollen can lead to fruit set, although cross- pollination typically results in higher seed set, larger fruits, and greater yield (DeVetter et al. 2022; Chabert et al. 2026). Thus, while the contribution of ants to blueberry pollination may be limited by their lower efficiency in pollen deposition and tendency to promote self-fertilization, they may still play a valuable contribution under conditions in which flying pollinators are scarce, such as during unfavourable weather or at early flowering stages, particularly if ants are present in large numbers.

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Author contribution

Helena Castro: Conceptualization; investigation; data analysis; supervision; writing – original. Catarina Moniz: investigation. Arminda Lopes: Plant management; Writing – review and editing. João Loureiro: Writing – review and editing. Sílvia Castro: Supervision; writing – review and editing.

Disclosure statement

The authors declared no competing interests.

Generative AI disclosure statement

No AI tools were used.

Data availability statement

Data will be made available upon request to the corresponding author.

Appendices

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

Table S1. Meteorological data.

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