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3D-printed flowers for standardised pollinator monitoring

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ABSTRACT

Global declines in insect pollinators have triggered the need for standardised, scalable methods to monitor pollinator populations. Automated photomonitoring and machine-learning-based identification are emerging as promising non-lethal approaches for large-scale insect observation, but their effectiveness requires reliable and consistent monitoring designs. Artificial flowers offer a solution to limitations associated with natural flowers, including variability in floral availability, lack of standardisation, and wind-induced noise in visual data, yet their performance under real field conditions remains largely untested.

Here, we developed 3D-printed artificial flowers, using *Malva multiflora* (Malvaceae) as a model species, incorporating increasingly complex sensory cues and rewards. We evaluated their performance by comparing insect pollinator species richness and visitation rates in artificial and co-occurring natural flowers using visual observations across 16 field sites in Southern Spain. Although artificial flowers received four times fewer species and visits per flower than natural flowers, they nonetheless accounted for around 50% of all recorded species. Variation in sensory cues among artificial flower treatments had little influence on attractiveness. Importantly, pollinator richness and visitation rates on artificial and natural flowers were strongly positively correlated, indicating that artificial flowers can provide reliable relative indicators of pollinator diversity and activity. Smaller-bodied bee species and those with warmer climatic affinities were more likely to visit artificial flowers, suggesting trait-based differences in exploratory behaviour or floral discrimination.

Our findings demonstrate the potential of 3D-printed artificial flowers, showing that, while not direct substitutes for natural flowers, they can function as effective, reproducible, and scalable tools for standardised pollinator monitoring.

1. Introduction

The ecological and economic importance of pollinating insects in sustaining plant reproduction and agricultural productivity is widely recognised (Artamendi et al., 2025; Murphy et al., 2022), yet numerous studies over recent decades have highlighted the severe threat they face from global change drivers (Potts et al., 2010; Wagner et al., 2021). These findings have prompted widespread calls for systematic, long-term monitoring of pollinator communities to guide conservation and management strategies (Dicks et al., 2016; Potts et al., 2016). For example, large-scale initiatives such as the EU Pollinator Monitoring Scheme (EU-PoMS) in Europe, the USGS Pollinator Science Strategy (2025–2035) in the United States, and the Investigation and Evaluation of Pollinator Insect Resources in eastern China (Luo et al., 2026) have been developed to standardise pollinator monitoring at continental scales. These programmes align with emerging policy frameworks such

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as the EU Nature Restoration Regulation (Stout and Dicks, 2022). Traditionally, these pollinator monitoring schemes have relied on labour-intensive and often invasive lethal methods, including hand-netting, pan trapping, and direct observation by trained experts (O'Connor et al., 2019). These techniques are time-consuming, require taxonomic expertise, and are difficult to standardise across regions, habitats, and observers. Therefore, there is a growing demand for innovative, non-lethal, and ideally automated approaches to monitor pollinator diversity and activity efficiently (Klink et al., 2022).

Camera-based photomonitoring has emerged as a promising tool for quantifying pollinator visitation (Watazu et al., 2025), using time-lapse or motion-triggered imaging to record insect visits to flowers (Besson et al., 2022; Darras et al., 2024; Naqvi et al., 2022). This method enables continuous, non-invasive monitoring of pollinators in the field and can be integrated with computer vision and machine-learning algorithms for automated identification (Høye et al., 2021; Steen, 2017). However, camera-based approaches often face several challenges when monitoring pollinators visiting natural flowers, including spatio-temporal variation in floral availability, lack of standardisation across study sites, and wind-induced movement that generates false detections in automated systems (Watazu et al., 2025). In addition, the natural arrangement of flowers often yields only partial body views in photographs, limiting the effectiveness of camera-based photomonitoring (Watazu et al., 2025). In this context, 3D-printed flowers provide a novel, standardised, cost-effective, and customisable sampling approach. They can reduce variation associated with natural bloom dynamics, provide physical stability (minimising false detections from wind-induced movement), and avoid potential climate-related constraints on flowering, while remaining easily replicable and shareable across users (Walker and Humphries, 2019). Because artificial flowers can be designed with or without rewards, they also minimise double-counting in automated monitoring systems. Therefore, artificial flowers might offer a promising avenue for conservation science by enabling robust comparisons across sites, regions, and time. This is particularly relevant for large-scale photomonitoring programmes and policy frameworks, which require harmonised, scalable, and repeatable methodologies to detect biodiversity change and evaluate management actions.

Artificial flowers have already been used to explore pollinator preferences for floral traits (Chapman et al., 2023; Lunau et al., 1996; Raine and Chittka, 2007), assess learning behaviour (Baek et al., 2024; Chittka and Thomson, 1997; Spaethe et al., 2001), and test responses to specific visual and olfactory cues (Campos et al., 2015; Ferrero et al., 2025; Lawson et al., 2018; Policha et al., 2016; von Arx et al., 2012). However, the ecological validity of artificial flowers as proxies for real flowers remains largely untested. It is unclear whether 3D-printed flowers can replicate the attractiveness of natural flowers, accurately represent visitation rates, or attract comparable communities, unbiased in their composition. Real flowers are inherently complex, multisensory systems combining visual, olfactory, tactile, thermal, and humidity cues to facilitate detection and recognition of (sometimes learnt) features by pollinators (Raguso, 2008; von Arx et al., 2012; Whitney et al., 2009). These cues often act synergistically and have evolved under strong pollinator-mediated selection, reliably signalling floral profitability and facilitating efficient foraging (Kessler et al., 2015; Schiestl and Johnson, 2013). Different pollinator species rely on different sensory combinations. For example, hawkmoths use floral scent and shape under low–light conditions (Goyret et al., 2007), whereas wild bees often prioritise colour, pattern, or inflorescence architecture (Ishii et al., 2008; Makino and Sakai, 2007; Reverté et al., 2016). Even subtle shifts in such floral traits can markedly alter pollinator behaviour (Campos et al., 2015; Dyer et al., 2007; von Arx et al., 2012). Therefore, the composition of pollinator communities observed on artificial flowers might considerably differ from that on real flowers, particularly because pollinator traits can also shape exploratory behaviour and foraging decisions, influencing the probability of visits to novel or imperfect resources such as artificial flowers. Body size, for example, correlates with flight capacity, perception (Spaethe and Chittka, 2003), and energetic demand, i.e. larger species can better discriminate among resources but incur higher costs from unrewarded visits (Kendall et al., 2019). Sociality may also promote exploratory behaviour, as social species typically forage over wider ranges and can better afford occasional foraging errors compared to solitary taxa (Grüter and Hayes, 2022; Kortsch et al., 2023). Similarly, nesting strategy and the use of plant materials can further affect responsiveness to floral cues by reducing the perceived risk or cost of exploration. These interspecific differences likely moderate species' engagement with artificial flowers. Understanding which floral and pollinator traits govern attraction, and how pollinator traits predict the likelihood of visiting artificial flowers, is therefore key to designing realistic and ecologically meaningful artificial-flower systems for monitoring.

In this study, we used a model species, *Malva multiflora* (Cav.) Soldano, Banfi & Galasso (Malvaceae), to experimentally evaluate the field performance of 3D-printed flowers. We manipulated individual floral traits, including human-visible colour, ultraviolet (UV) reflectance, and nectar reward, to assess their effects on pollinator attraction. By comparing insect visitation rates and community composition between artificial treatments and co-occurring natural flowers, we evaluated whether 3D-printed flowers can serve as reliable proxies for natural blooms in pollinator monitoring. Specifically, we tested the following hypotheses: (*H1*) Artificial flowers are visited by a substantial subset of the pollinator species visiting natural flowers, although overall richness is higher in real flowers; (*H2*) Artificial flowers with more realistic visual and chemical cues (e.g., UV reflectance, and nectar) are visited by more species than simpler designs; (*H3*) Individual visit durations are shorter on artificial flowers than on real flowers, reflecting their reduced overall realism; (*H4*) Functional traits of pollinators, such as body size, thermal niche, degree of sociality, and nesting behaviour, predict which pollinator species are more likely to visit artificial flowers, and (*H5*) Despite lower absolute richness and visitation rates, pollinator richness and visit frequency on artificial flowers correlate positively with those on real flowers, supporting their utility for standardised monitoring.

2. Materials and methods

2.1. Study system and sampling sites

This field experiment was conducted in Granada (Andalucia), Southern Spain, within a heterogeneous landscape dominated by traditional olive farms and semi-natural Mediterranean shrubland (37°11′ N -3°59′ W, and an altitude of ~600 m.a.s.l). The region was selected because previous research has identified it as a hotspot of pollinator richness in Europe (Bartomeus et al., 2024; Martínez-Núñez et al., 2020; Cano et al., 2024). The area has a Mediterranean climate, characterised by hot, dry summers and mild, wet winters. Local herbaceous communities are dominated by annual species typical of the Guadalquivir Basin and the wider Mediterranean lowlands (Tarifa et al., 2021). In this landscape, we selected 16 sites, where the focal species (i.e., *M. multiflora*) and other flowering species (i.e., high floral availability) were abundant.

2.2. Artificial flowers

We used *M. multiflora* as the model species because it is a widespread pan-Mediterranean generalist plant that is visited by a diverse range of pollinators, such as bees (including both solitary and social species), hoverflies, and, to a lesser extent, by beetles and butterflies. It has a wide phenology allowing its study for most of the growing season, is well studied in the region, and exhibits moderate floral complexity, making it suitable for replication using various printing materials (Fig. 1). In addition, to promote further research on artificial flower systems, we provide high-quality, ready-to-print 3D models (in .stl file format) for

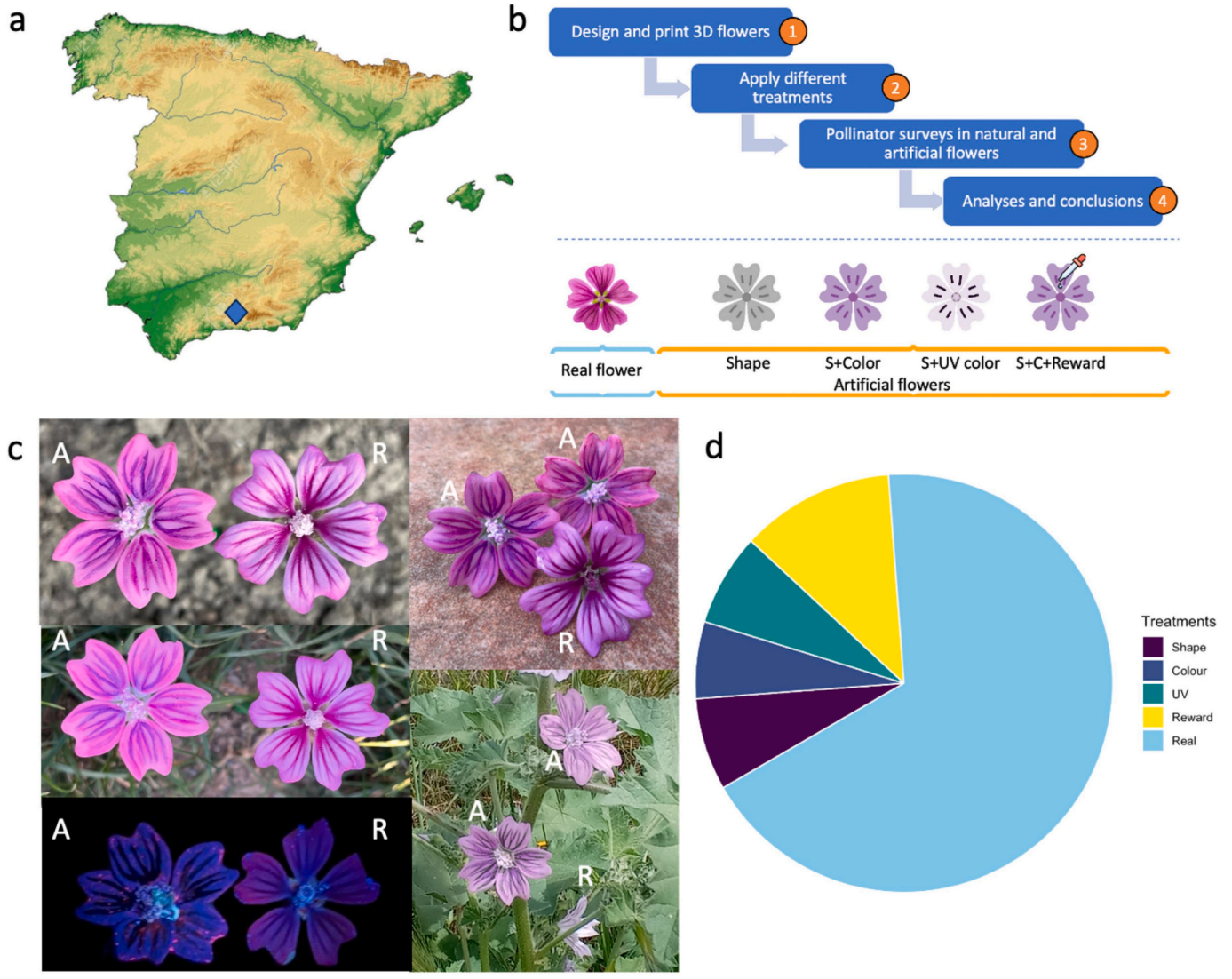

Fig. 1. Study area, experimental design, and descriptive measures. (**a**) Study area in Granada, Southern Spain. (**b**) Experimental design, showing the workflow and different experimental treatments. Treatments were not fully nested because colour and UV colour are mutually exclusive when assessed with the human eye (**c**) Artificial [A] vs. real [R] flowers under sunlight in the field and under 325 nm UV light (bottom left row). (**d**) Number of visits to artificial vs real flowers with different treatments.

five common and morphologically diverse wildflower species widely distributed in Europe and the northern hemisphere (see Fig. S1; and supplementary data). To approximate natural floral traits and assess the contribution of individual cues to pollinator attraction, we designed 3D-printed flowers and subjected them to four experimental treatments of increasing sensory complexity: (i) Shape only: Flowers were printed in white polylactic acid (PLA) filament and left unpainted, displaying only the structural shape of the flower without colour or any chemical cues added. This baseline isolates the role of morphology; (ii) Colour (visible spectrum): Flowers were painted with watercolours (*Jovi* brand; non-toxic and with minimal odour) to match the natural colour of *M. multiflora* blooms. Watercolours were selected to minimise artificial odour contamination compared to stronger or acrylic paints, and painted flowers were air-dried for a week before deployment; (iii) Colour + Ultraviolet (UV) reflectance: To replicate the UV patterns that often signal nectaries, real flowers were photographed in a dark room under a UV flashlight using a camera fitted with a 625 nm filter. Observed UV patterns, using UV filters, were then painted onto artificial flowers with non-toxic UV-reflective paint (*Moon Glow* brand); and (iv) Colour + Reward: These flowers contained a drop (5 μL) of 40% sucrose with 5% honey to provide an energetic reward and mild nectar-like amino acids and flavour cues that encourage naturalistic visitation and scent-reward association, within the artificial flower foraging framework (Spaethe et al., 2001). This volume falls within the natural range of nectar volume often observed in *M. multiflora* flowers (3–8 μL). Nectar rewards were replenished between sampling sessions but not between visits within a session, thereby mimicking natural resource depletion. In addition, real pollen collected from field specimens was placed on the artificial anthers to enhance ecological realism. This final treatment combined visual and chemical cues associated with floral rewards that pollinators can learn.

2.3. Experimental design and sampling protocol

At each of the 16 field sites, a single plant was selected. The four artificial flowers were then affixed to the same plant, mimicking the position of natural blooms (see Fig. 1). The same artificial flowers were used throughout the entire study. Treatments were assigned to separate stems (approximately 30–40 cm apart) within the same plant to control for plant-level variation. The plant was not manipulated or damaged (e.

g., real flowers were not removed), aside from the placement of the artificial flowers. On the selected plant, we observed three natural flowers and four 3D-printed flowers (one per treatment) continuously for 120 min (32 h in total) on sunny days without strong wind (Beaufort scale <5). The experiment was repeated for 16 days spanning the flowering season of the focal species (mid-April to late May 2025), with one site surveyed per day. All surveys were conducted between 11.00 and 17.00 h, coinciding with peak diurnal pollinator activity in the region during this period (e.g., Martínez-Núñez et al., 2020; Cano et al., 2024). To ensure spatial independence, sites were separated by at least 250 m (Fig. S2). We recorded all pollinator species (i.e., individuals contacting the reproductive structures of flowers) from the orders Hymenoptera, Lepidoptera, Coleoptera, and Diptera, and identified them to species level where possible (Table S1). We quantified visitation by recording the number of visits per flower and the duration of each visit. We additionally noted "checks" or approaches (i.e., instances in which a pollinator closely inspected a flower without landing) as an indicator of partial attraction; these were not included as visits in subsequent analyses. Most insects were captured using a sweep net for taxonomic identification, while minimising disturbance to ongoing foraging activity.

2.4. Pollinator species traits

We compiled four functional traits for bee species based on Miličić et al. (2026), where methodological details are fully described. The selected traits were chosen for their potential influence on exploratory behaviour and responsiveness to novel floral stimuli. Specifically, we considered: (i) *Body size*: estimated using intertegular distance as a proxy for overall size and flight capacity, perceptual range, and resource detection; (ii) *Species temperature index (STI)*: defined as the mean temperature across each species' European distribution, representing their thermal niche (Devictor et al., 2008). Warm-adapted species are generally more active under warmer or variable conditions, potentially increasing their likelihood of visiting artificial flowers; (iii) *Nesting material use*: used to distinguish species that incorporate plant material in nest construction. Such species may be more familiar with non-floral plant structures, potentially reducing their propensity to land on artificial flowers; and (iv) *Sociality*: categorised as solitary, parasocial, eusocial, or cleptoparasitic. Social species often tolerate higher exploratory risk, increasing their likelihood of exploiting unfamiliar floral resources.

2.5. Statistical analysis

All the analyses were run in the R statistical software V4.4.2 (R Core Team, 2024).

To test hypotheses *H1–H3*, we fitted three separate generalised linear mixed-effects models (GLMMs) with the 'lme4' package (Bates et al., 2015), with *pollinator species richness per flower*, total *number of visits per flower*, and *time spent per visit* as response variables. For all models, *flower type* (five levels: real, artificial shape, artificial colour, artificial UV colour, and artificial reward) was included as an explanatory variable, and sampling date (and therefore site) was included as a random intercept to account for repeated sampling and site-level variation. Models were fitted using restricted maximum likelihood [REML] estimation with a Poisson error distribution, appropriate for count data, and real flowers were considered the reference category. The effects of *flower type* on each response variable were then assessed using pairwise contrasts (Tukey-adjusted) of estimated marginal means (EMMs) obtained with the 'emmeans' package (Lenth, 2023). Predicted values with 95% confidence intervals were extracted and visualised using the 'ggeffects' package (Lüdecke, 2018). To further evaluate pollinator responses to the different flower types (*H2*), we fitted an additional model testing whether the proportion of inspections (or "checks"), where pollinators approached or inspected a flower without subsequently landing on it, differed among flower treatments. In addition, we performed a non-metric multidimensional scaling (NMDS) analysis using the 'metaMDS' function to compare the similarity in community composition of visiting insects between artificial and real flowers, and to assess the constancy of these communities across sites and sampling dates for both flower types. To evaluate the adequacy of our sampling effort and compare species accumulation rates between real and artificial flowers, we generated species accumulation curves for each flower type and estimated asymptotic species richness using the 'iNEXT' package (Hsieh et al., 2016). We visualised accumulation curves and estimated sampling coverages.

To test hypothesis *H4*, we then assessed whether bee traits predicted the propensity to visit artificial flowers by modelling the proportion of visits to real versus artificial flowers using beta regression generalised additive models (GAMs) with a logit link, implemented in the 'mgcv' package (Wood, 2017). Separate models were fitted for each trait: *body size* (intertegular distance, $n = 26$ species), *species temperature index* (STI, n = 26), *nesting material use* ($n = 24$; plant material, yes = 13 and no = 11), and sociality ($n = 27$; solitary = 19, parasocial = 1, eusocial = 3, or cleptoparasitic = 4). Genus was included as a random effect in these models, and total visits per species were used as model weights. Model fits were assessed through explained deviance and partial-effect plots. Residual diagnostics for all relevant analyses confirmed that assumptions of error distribution, independence, and homoscedasticity of residuals were met.

Lastly, to test hypothesis *H5*, we examined the relationship between species richness and visitation rates recorded on real versus artificial flowers across dates (or sites) using Spearman's ρ. To evaluate robustness, we conducted a leave-one-out (jackknife) sensitivity analysis, recalculating correlations after sequentially removing each observation.

3. Results

Across all sites, we recorded 487 interactions between insect pollinators and flowers (Fig. S3). At the study scale, a cumulative total of 45 different pollinator species were observed landing on flowers (see Table S1 for the full list of species), of which 22 occurred exclusively on real flowers, and 23 visited both real and artificial flowers (Fig. 2a). Therefore, the community of visiting insects in artificial flowers was fully nested within the community of insects visiting real flowers (Fig. S4). Insects from four different insect orders visited the artificial flowers, with Hymenoptera being the most active pollinators in both artificial and real flowers (Fig. S5). Within Hymenoptera, *Lasioglossum*, *Chelostoma*, *Eucera*, *Ceratina*, and *Andrena* were the most active genera (Fig. S6). Species visiting real flowers were more consistent across days and sites, whereas those visiting artificial flowers (all the treatments combined) showed greater stochasticity (Fig. 2b), but stabilised over time (i.e., high overall coverage, see below).

Mixed-effects models revealed that, at the individual flower scale, real flowers were visited by nearly four times more pollinator species (predicted mean, $\mu = 3.86$, 95% confidence intervals, CIs = 3.29–4.54) and received six times as many visits ($\mu = 6.71$, 95% CIs = 5.42–8.31) as artificial flowers (Fig. 3a, b). Pollinators also spent significantly more time on real flowers ($\mu = 9.31$ s, 95% CI: 8.03–10.80) than on artificial ones. Among artificial treatments, "shape-only" flowers yielded the longest visits ($\mu = 5.84$ s, 95% CIs = 4.42–7.73), whereas "UV" flowers received the shortest (see Fig. 3c; $\mu = 3.61$ s, 95% CIs = 2.60–5.01). Different treatments of artificial flowers received a similar number of visits and species. Furthermore, the probability of inspections ("checks") that did not result in floral visits (landings) was significantly higher for artificial flowers compared to real flowers, whereas no differences were found among the artificial treatments (Fig. S7).

Species accumulation curves showed that real flowers accumulated more pollinator species, while artificial flowers reached asymptotes more quickly (Fig. 3d). In addition, real flowers reached an estimated coverage of 94%, whereas artificial flowers reached ~85%.

Generalised additive models showed that bigger species preferred

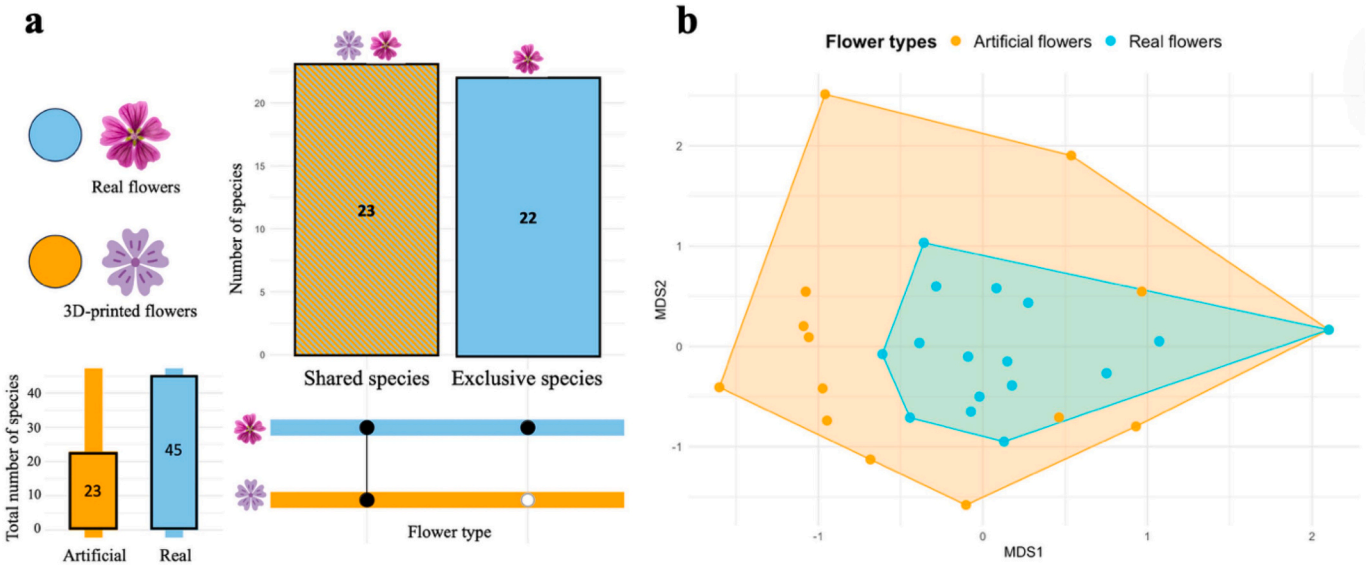

Fig. 2. Comparison of species composition across real and artificial flowers. (**a**) Total number of insect visitor species recorded on real flowers (blue) and 3D-printed flowers (orange), partitioned into shared (striped) and exclusive (solid) components. All species recorded on artificial flowers were also observed on real flowers, indicating the absence of unique species associated with artificial flowers. (**b**) Non-metric multidimensional scaling (NMDS) ordination of pollinator community composition across sampling units (each point represents a site × date combination). Convex polygons illustrate the dispersion of communities associated with real (blue) and artificial (orange) flowers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

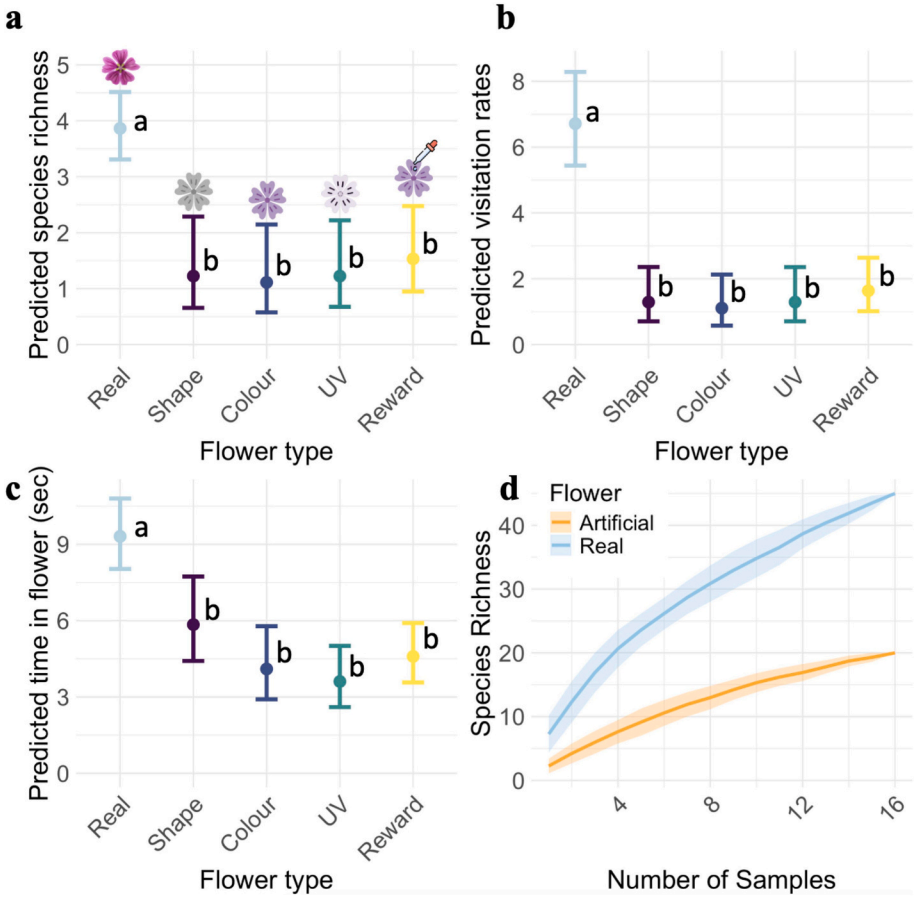

Fig. 3. Differences in pollinator visitations between real and artificial flowers. Model-predicted means and 95% confidence intervals are shown for (**a**) species richness, (**b**) flower visitation rates, and (**c**) time spent by flower visitors in each artificial flower type and real flowers. (**d**) Species accumulation curves in real vs. artificial flowers across sampling days (sites). Statistical significance is interpreted as the non-overlap of the 95% CIs between any pair of flower types.

real flowers more than smaller species (Fig. 4a, marginal deviance explained = 8%, conditional deviance explained = 80%). More cold-adapted species preferred real flowers, while more warm-adapted species tended to proportionally visit more artificial flowers than cold-adapted species (Fig. 4b, marginal deviance explained = 17%, conditional deviance explained = 73%). Species that use plant material to build their nests also preferred real flowers, while species that do not use plant materials visited artificial flowers more often than species that use plant material (Fig. 4c). We found no significant evidence that the degree of sociality in bees affected their choice regarding artificial and real flowers in our experiment (Fig. 4d).

Species richness recorded across sites was significantly and positively correlated between real and artificial flowers (Fig. 5a; Spearman's $\rho = 0.63$, $P = 0.008$, $N = 16$, df = 14). Leave-one-out sensitivity analysis further confirmed that this relationship is robust (Spearman's ρ range: 0.55–0.73, all $P < 0.05$). Similarly, visitation rates were strongly correlated between real and artificial flowers (Fig. 5b; Spearman's $\rho = 0.73$; $P = 0.001$, N = 16, df = 14), with jackknife correlations remaining positive (Spearman's ρ range: 0.70–0.81, all $P < 0.05$).

4. Discussion

Our study demonstrates both the potential and the limitations of 3D-printed artificial flowers as tools for monitoring pollinator communities in the field. By directly comparing real and artificial flowers, we assessed whether artificial models can reproduce patterns of pollinator richness and visitation observed in nature, and evaluated how floral traits (i.e., shape, colour, UV reflectance, and reward) and pollinator traits (i.e., body size, thermal niche, nest material use, and degree of sociality) affect pollinator responses. As expected, real flowers consistently attracted more species and visits than artificial flowers, confirming that these artificial flowers cannot fully deceive pollinators. Nevertheless, artificial flowers were not ignored and received visits from a broad subset of the pollinator community. Importantly, species richness and visitation rates recorded on real and artificial flowers were strongly correlated. This suggests that although artificial flowers cannot entirely

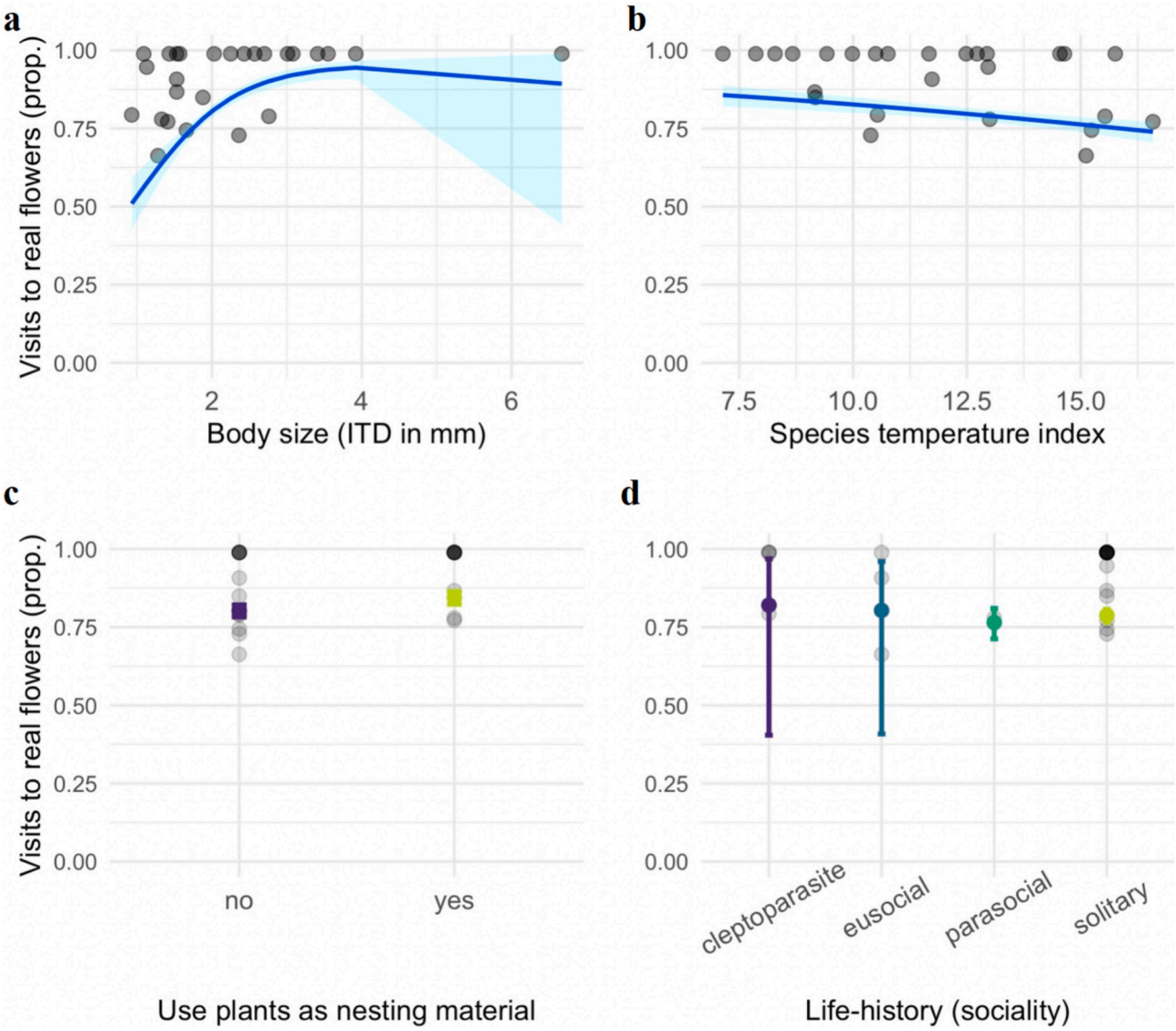

Fig. 4. Predicted relationships between bee species traits and the proportion of visits to real vs. artificial flowers. Smoothed relationships between the proportion of visits to real vs. artificial flowers and (**a**) body size (ITD, intertegular distance), and (**b**) species temperature index. The shaded areas around the fitted curves represent 95% confidence intervals. Model-predicted means (±95% confidence intervals) for the relationships between visits to real vs. artificial flowers and (**c**) use of plant material for nesting, and (**d**) sociality. Statistical significance is interpreted as the non-overlap of the 95% CIs. Transparent grey points show raw data values.

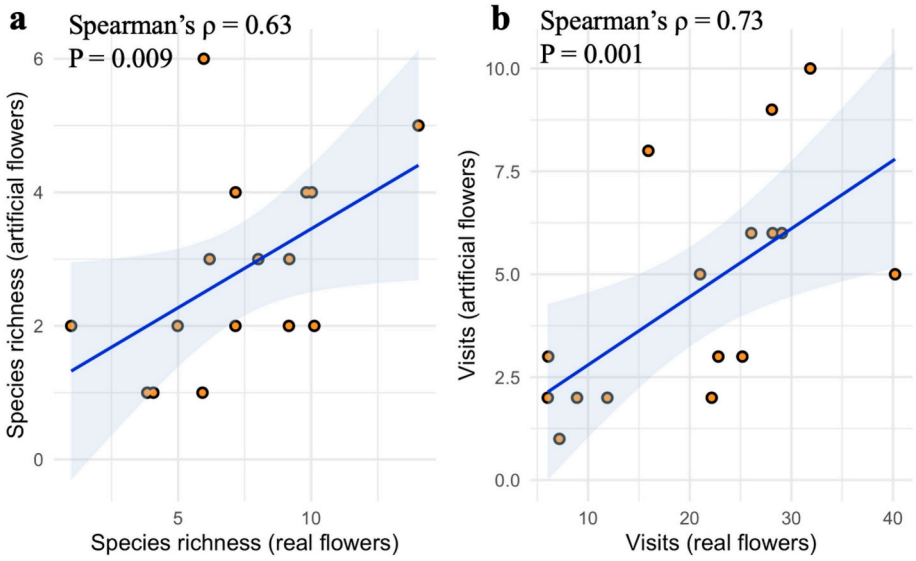

Fig. 5. Relationship between observations in real and artificial flowers across days (and sites). Spearman correlation test of (**a**) species richness, and (**b**) visitation rates in real and artificial flowers. For readability, values show average richness and visits for real flowers ($N = 3$ per day) but cumulative values for artificial flowers ($N = 5$ per day). The x-axis is trimmed (it starts at 5 and not at 0) in panel b for enhanced visualisation. The experiment was repeated 16 times on different days and sites, hence, $N = 16$. The blue line represents the fitted linear regression with 95% confidence intervals, illustrating the positive relationship between the variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

represent the actual pollinator diversity, abundance and community composition on real flowers, they may still serve as a reliable indicator for tracking relative changes in pollinator diversity and activity across space and time.

4.1. *Effectiveness and sensory limitations*

We expected to find more pollinators on real flowers (*H1*), which was supported by our results, as species richness was substantially higher on real flowers, which were visited by nearly four times more species per flower and received six times more visits per flower than artificial ones. To our knowledge, this is the first field-based study to directly benchmark pollinator visitation rates and taxonomic richness between artificial and real flowers under comparable conditions. These results highlight the central role of complex floral traits in structuring pollinator interactions (Hemingway et al., 2024). Natural flowers provide a multisensory suite of cues, including colour, pattern, texture, scent, temperature, chemical signals, humidity, and electric charge that artificial flowers typically fail to fully replicate (Harrap et al., 2017; Herrera, 2024; Seymour et al., 2003; von Arx et al., 2012). The difficulty of deceiving pollinators with artificial flowers underscores how strongly these animals rely on fine-scale perceptual abilities to evaluate floral authenticity (Chittka and Thomson, 2001). Experimental evidence further shows that innate floral object recognition in some pollinators depends on the integration of both visual and olfactory cues, reinforcing the importance of multimodal signalling for effective attraction (Mishra et al., 2025). Landing on unrewarding artificial flowers likely incurs a measurable cost for the pollinators, due to wasted energetic expenditure. Trade-offs between visitation rate and energy cost are well supported by previous foraging efficiency studies (Balfour et al., 2015; Roddy, 2019). In addition, when encountering an unfamiliar flower type, pollinators weigh potential energetic gain against uncertainty, as unfamiliar resources may carry unrewarding risks such as exposure to predators or pathogens (Dukas, 2001; Nicholls et al., 2022; Reader et al., 2006). The relatively high frequency of "checks" that did not result in landings (Fig. S7) further reinforces the idea that our artificial flowers lack crucial elements of attraction, recognition or reward necessary to sustain similar visitation rates as real flowers. Despite the fact that one of the treatments provided nectar and pollen, it seems that the perceived risks did not outweigh the perceived energetic gain in the short term. Nevertheless, despite the relatively poor capacity to deceive pollinators compared to real flowers, nearly half of the species recorded on natural flowers also visited artificial 3D-printed ones, suggesting that artificial flowers can still attract an ecologically meaningful subset of pollinators. In fact, a recent study has shown that artificial flowers can attract more pollinators than other commonly used methods, such as pan traps or coloured paper squares (Ash et al., 2026).

4.2. *Limited effect of multimodal cues*

Contrary to our hypothesis (*H2*), incorporating more sensory dimensions (i.e., UV reflectance) or incentives (i.e., reward) did not significantly increase the number of visits or visiting species. This contrasts with previous experiments showing that multimodal cues enhance pollinator visitation to artificial flowers (Chapman et al., 2023). This finding suggests that in natural flower-rich settings, pollinators may have little incentive to invest in exploring novel or risky options, regardless of their sensory complexity (Goulson, 1999; Raine and Chittka, 2007). At the same time, there were many short visits (~3 s) of pollinators to artificial flowers. These short visits may reflect a perceived lack of reward or imperfect floral mimicry, leading to quick post-landing rejection. Instead, they may arise from generalised decision rules: insects often respond to coarse visual or spatial cues such as floral shape, orientation, or placement on vegetation before discriminating at finer sensory scales (Chittka and Thomson, 2001; Spaethe et al., 2001). Some exploratory landings may also reflect a strategy of "low-cost sampling", where pollinators balance the risk of wasting time or energy against the potential benefit of discovering a novel reward. Taken together, our findings indicate that simpler artificial flowers perform comparably to more elaborate designs in attracting pollinators, which is encouraging for studies that require large numbers of standardised but easily prepared visual stimuli. Nonetheless, broader inference will require further studies across different habitats and regions that vary in floral resource availability and community structure. In particular, variation in floral availability has been shown to influence sampling outcomes in widely used methods such as pan traps (Krahner et al., 2024), and may influence pollinator responses to artificial flowers, too, as neighbouring floral resources can either attract or divert

pollinators depending on their relative density and attractiveness (Holzschuh et al., 2011; Gilpin et al., 2022). These effects should therefore be explicitly quantified in future work.

As hypothesised, visits were significantly shorter on artificial than on real flowers (*H3*), likely because pollinators quickly notice the absence of multisensory cues such as scent, floral texture or thermal similarity. Among artificial treatments, shape-only models yielded the longest visits. These patterns further highlight that real flowers offer a combination of multisensory and tactile cues that artificial models cannot easily reproduce without substantial effort or technological complexity (Dyer et al., 2006; Leonard et al., 2011). This finding has important practical implications for camera-based monitoring when using interval photography or time-lapse cameras. Short visits substantially reduce the probability of capturing pollinator visits, as the discrete nature of interval photography often leads to an underestimation of visit frequency compared to continuous observation, even in real flowers (Watazu et al., 2025). Therefore, extending the visit duration on artificial flowers is crucial for the effective implementation of these photomonitoring applications. Alternatively, motion-induced photography might be better suited for capturing these rapid floral interactions (e.g., Steen, 2017).

4.3. Trait-based patterns of exploratory behaviour

The observed trait associations suggest that exploratory tendencies toward artificial flowers are not random but partly structured by species' functional characteristics (*H4*). Smaller-bodied bees and those with warmer climatic affinities were more likely to visit artificial flowers. This supports the idea that smaller species might have a constrained perception and lower discerning capacities compared to larger species (Spaethe et al., 2001), and that thermal tolerance expands foraging ranges, promoting inspection of novel or suboptimal resources (Kendall et al., 2019; Kortsch et al., 2023). Similarly, species that use plant material for nesting may rely more strongly on structural or tactile plant cues, potentially influencing their response to simplified artificial flowers. This interpretation is consistent with evidence that pollinator responses to floral stimuli depend on prior experience and learned cue associations (Forrest and Thomson, 2009; Menzel, 1999). These behavioural responses may underpin broader exploratory or risk-tolerant foraging strategies (Raine and Chittka, 2008). Our results thus suggest that species-level traits can predict responsiveness to novel floral stimuli, highlighting an often-omitted dimension of trait-based filtering in pollinator monitoring systems (Prendergast et al., 2020).

4.4. Monitoring pollinators with artificial flowers: future directions and applications

Our results show that both species richness and visitation rates in artificial flowers positively correlate with those in real flowers across sites and dates (*H5*), despite the lower absolute attractiveness of artificial compared to natural flowers. In addition, the community of species visiting artificial flowers was a nested but functionally biased subset of the species visiting real flowers. This pattern of "methodological filtering" is consistent with other standardised sampling techniques, such as pan trapping or trap-nesting, which typically capture specific taxonomic or functional slices of the local community rather than the full assemblage (Westphal et al., 2006; Prendergast et al., 2020). Consequently, while these artificial flowers may not fully substitute real flowers in estimating pollinators' absolute abundance or richness, they offer a scalable, standardised, and cost-effective tool for monitoring relative temporal trends and site-level differences, serving as a standardised indicator of pollinator activity and diversity.

To our knowledge, this study provides the first experimental field assessment of 3D-printed flowers as proxies for real blooms, offering a foundation for future work. Nevertheless, several limitations remain. First, our experiment focused on a single model species (*M. multiflora*) in a single ecological context; future work should test whether the patterns observed here generalise across a broader range of plant taxa, habitats, and especially environments with contrasting available resources. To facilitate such efforts, we provide professionally designed, high-quality 3D-printable models for five common wildflower species (see Fig. S1; and supplementary data), enabling wider adoption as well as broader testing and refinement of this approach. These models offer a highly economical and scalable method. Printing time is relatively fast (~ 20 min per 10 units), material cost can be very low (typically <0.30 EUR per flower), and a printing machine is economic too, making immediate upscaling feasible for large-scale field arrays without significant technological innovation. We strongly recommend using bio-based, organic materials, such as maize-based polylactic acid (PLA), for production, as pollinators actively avoided artificial flowers printed in synthetic resins in our system, likely due to residual chemical odours (see Supplementary Material for more details).

Regarding field application, we advise deploying a relatively high density of flowers per site as the utility of this method relies largely on the accumulation of exploratory visits over time; therefore, using larger numbers ensures a sufficient sample size to capture representative pollinator data. Ultimately, we envision this approach as particularly well-suited for long-term pollinator monitoring in sensitive habitats where non-lethal sampling is required, or for experimental studies that necessitate the isolation of specific floral traits. Initial trials suggest that the performance of artificial flowers may depend on the baseline attractiveness of the focal species, underscoring the importance of careful species selection in future applications. In addition, our deployment involved attaching artificial flowers directly to living plants, which may have enhanced their detectability. Isolated flowers may attract fewer visitors, potentially requiring longer sampling periods to reach high sample completeness. Moreover, the availability of natural floral resources likely shapes pollinator engagement with artificial flowers, a factor that warrants more detailed investigation. Lastly, several improvements could further increase the realism and attractiveness of artificial flowers, although often at the cost of accessibility. For example, it would be possible to incorporate scent by adding whole floral bouquets obtained via solvent extraction (e.g., Haber et al., 2019), and to use spectrometric measurements to match colours to bee-perceived spectra and therefore increase visual fidelity (e.g., Jersáková et al., 2012). For instance, recent advances in robotic flower systems demonstrate how integrating multimodal signalling and real-time sensing can expand the experimental possibilities of artificial flowers, although such approaches typically involve greater technological complexity and cost (Foley et al., 2025). However, our results demonstrate that our simpler, accessible, and time-efficient method can still yield highly informative outcomes.

In conclusion, although 3D-printed artificial flowers in our study did not fully replicate the attractiveness of natural flowers, they overall attracted a substantial number of visits and species and closely mirrored the relative patterns observed in real flowers. This supports their use as a promising tool for pollinator monitoring and experimental studies, offering an economical, reproducible, and scalable approach to capturing variation in pollinator richness and visitation, and, when coupled with photomonitoring, an ethically preferable (non-lethal) complement to traditional methods.

CRediT authorship contribution statement

Carlos Martínez-Núñez: Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Rocío Sánchez-López:** Methodology, Investigation. **Domingo Cano:** Methodology, Investigation. **Antonio Pérez:** Methodology, Investigation. **Felix Neff:** Writing – review & editing, Methodology, Investigation. **Corina Maurer:** Writing – review & editing, Methodology, Investigation. **Tharaka Priyadarshana:** Writing – review & editing, Methodology, Investigation. **Murray**

Hamilton: Writing – review & editing, Methodology, Investigation. **Atushi Ushimaru:** Writing – review & editing, Methodology, Investigation. **Chao-Dong Zhu:** Writing – review & editing, Methodology, Investigation. **Oliver Schweiger:** Writing – review & editing, Methodology, Investigation.

Declaration of Generative AI and AI-assisted technologies in the writing process

No Artificial Intelligence was used to generate any content in this article.

Declaration of competing interest

Authors do not have conflicts of interest to disclose.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.112007.

Data and code availability statement

All the data and source code, as well as the .stl files with five flower models ready for printing, are publicly available in a Zenodo repository: https://doi.org/10.5281/zenodo.17664213.

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