



Supporting wild *Osmia* populations in Mediterranean orchards: nesting success across different substrates and landscapes

Miguel Azevedo^{1,2,3} · Elisabete Figueiredo³ · Rafael Carvalho^{4,5} · Maria Teresa Rebelo^{1,2}

Received: 16 October 2024 / Accepted: 6 June 2025
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Abstract

Although artificial nesting substrates are increasingly used to support wild bee populations in agricultural landscapes, yet little is known about the spontaneous colonisation of such nests in Mediterranean orchards. This study evaluated the nesting behaviour of wild *Osmia* populations in apple, pear, and cherry orchards in Portugal, focusing particularly on how nest features and landscape structure influence colonisation patterns. Over two years, *Osmia caerulea* was the most abundant species, followed by *O. bicornis*. Overall occupancy rates were low across all orchard types, although higher colonisation was observed in cherry orchards, likely due to earlier flowering and greater habitat heterogeneity. In apple and pear orchards, both species preferred paper tubes: *O. caerulea* nested mainly in 6 mm cavities, whereas *O. bicornis* favoured 8 mm cavities and was most abundant in apple orchards. Brood viability was lower in *O. caerulea*, particularly in pine wood blocks. At the landscape scale, the success of the nests of both species was positively associated with the proportion of non-irrigated arable land and fruit tree cover within a radius of 500 m. *O. caerulea* also responded positively to land-use diversity, whereas *O. bicornis* favoured more urbanised orchard contexts. Despite the low colonisation rates observed, identifying *O. caerulea* and *O. bicornis* as the main trap nesting species highlights their potential as targets for future management programmes. Paper tubes performed best under the tested conditions, but broader trials are needed. Improving habitat quality in orchards is essential for supporting wild bee populations.

Implications for insect conservation

Understanding how wild *Osmia* species use trap nests provide insight into the current status of local populations and supports the development of targeted management measures to enhance their persistence in orchard landscapes.

Keywords Solitary bees · Agroecosystems · Nesting success · Trap nest · Crop pollination

✉ Miguel Azevedo
azevedo.mfs@gmail.com

Elisabete Figueiredo
elisalacerda@isa.ulisboa.pt

Rafael Carvalho
pcarv.rafael@gmail.com

Maria Teresa Rebelo
mtrebelo@ciencias.ulisboa.pt

¹ Ce3C-CHANGE - Centre for Ecology, Evolution and Environmental Changes and Global Change & Sustainability Institute, Faculdade de Ciências, Universidade de Lisboa, Lisboa 1749-016, Portugal

² CESAM – Centre for Marine and Environmental Studies, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, Lisboa 1749-016, Portugal

³ LEAF - Linking Landscape, Environment, Agriculture and Food, Laboratório Associado TERRA, Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, Lisboa 1349-017, Portugal

⁴ COTHN-CC - Centro Operacional e Tecnológico Hortofrutícola Nacional - Centro de Competências, Estrada de Leiria, S/N, Alcobaça 2460-059, Portugal

⁵ FLOWer Lab, Centro de Ecologia Funcional – Ciência para as Pessoas e o Planeta, Departamento de Ciências da Vida, Universidade de Coimbra, Calçada Martim de Freitas, Coimbra 3000-456, Portugal

Introduction

Insect pollination is a key ecosystem service that supports both biodiversity and agricultural productivity worldwide (Winfree et al. 2008, 2011; Garibaldi et al. 2014a, b; Klein et al. 2018; Reilly et al. 2020). The expansion of pollinator-dependent crops in recent years (Aizen and Harder 2009; Breeze et al. 2014; Aizen et al. 2019), has made us more reliant on insect pollination. Wild bees play a crucial role in this process (Klein et al. 2007; Winfree et al. 2008; Garibaldi et al. 2014a, b; Reilly et al. 2020). Although the European honeybee (*Apis mellifera*) is the most widely used pollinator in commercial agriculture, wild bees are often more effective, providing more consistent pollination in field conditions (Garibaldi et al. 2014a, b; Eeraerts et al. 2020b; Pisman et al. 2022). Nevertheless, pollination management strategies continue to rely predominantly on honeybees, reflecting a misconception that wild bees are less important in agricultural settings (Koh et al. 2016; Garibaldi et al. 2019; Rollin and Garibaldi 2019; Eeraerts et al. 2020b; Boyle et al. 2020; McKerchar et al. 2020). While honeybees can supplement crop pollination, they cannot fully replace the role of wild bees, which often exhibit complementary foraging behaviours and greater resilience to environmental variability (Garibaldi et al. 2014a, b; Goulson et al. 2015; Zhang et al. 2015).

Due to their complementary foraging behaviour, morphological traits, and phenological synchrony with crop flowering, wild bees play a particularly important role in the pollination of early-blooming fruit crops. This is particularly true of cherry (*Prunus avium*), almond (*Prunus dulcis*), apple (*Malus domestica*), and pear (*Pyrus communis*), all of which are widely cultivated in Mediterranean regions (Westrich 1990; Mallinger and Gratton 2015; Eeraerts et al. 2022; Kline et al. 2023). However, increasing pressure from agricultural intensification, habitat loss, and simplified landscapes reduces both floral and nesting resources for wild bee populations (Connelly et al. 2015; Potts et al. 2016; Hallmann et al. 2017; Kline and Joshi 2020; Eeraerts et al. 2021). Therefore, it is crucial to understand and enhance the role of wild pollinators in agricultural systems for the conservation of biodiversity and the implementation of Integrated Pest and Pollinator Management (IPPM) strategies (Kline and Joshi 2020; Pardo and Borges 2020).

Solitary bees of the genus *Osmia* (Hymenoptera: Megachilidae), which nest above ground, are among the most effective pollinators of temperate fruit trees. They have been widely used in managed pollination programmes, particularly in Europe and North America (Bosch and Kemp 2002; Bosch et al. 2006; Sedivy and Dorn 2013; Eeraerts et al. 2020b; Dainese et al. 2018; Hamroud et al. 2023). Several species, including *Osmia bicornis* (Linnaeus, 1758),

Osmia cornuta (Latreille, 1805), are commonly associated with European orchard systems (Bosch and Kemp 2002; Sedivy and Dorn 2013; Zajdel et al. 2024; Magnin et al. 2025). While most studies focus on reared populations, few have examined the nesting behaviour of spontaneous wild populations of *Osmia* species in the Mediterranean agroecosystems (Rosas-Ramos et al. 2017; Tobajas et al. 2022; Hamroud et al. 2023).

Artificial nesting structures, or trap nests, have been widely used to monitor and support cavity-nesting bees, particularly species of the genus *Osmia* (Bosch and Kemp 2002; Gruber et al. 2011; Sedivy and Dorn 2013; Eeraerts et al. 2020b; Belien et al. 2021; Bihaly et al. 2021). These nests mimic natural cavities and are made from materials such as drilled wooden blocks, hollow plant stems (e.g. bamboo and reeds), or paper tubes. Although traditional materials such as reeds and wood have been extensively studied, paper tubes have become increasingly popular in recent years due to their affordability and ease of use in sampling surveys (Joshi et al. 2020; Eeraerts et al. 2020a). However, their effects on nesting preference, brood development, and long-term reproductive success remain insufficiently studied. The structural features of trap-nests, such as cavity diameter and depth are known to influence offspring size, sex ratio and viability (Seidelmann et al. 2016). Furthermore, landscape composition and structure have been demonstrated to influence trap nest occupancy and brood development (Dainese et al. 2018; Staab et al. 2018; Tobajas et al. 2022). There is also evidence that climate change and habitat fragmentation can have both positive and negative effects on bee body size (Gérard et al. 2021; Prestele et al. 2021). Landscape composition and complexity are also known to strongly influence the nesting success of solitary bees. Heterogeneous landscapes typically tend to provide a wider variety of floral resources and suitable nesting materials, thereby increasing the rate at which artificial trap nests are colonised (Dainese et al. 2018; Staab et al. 2018). Conversely, simplified agricultural landscapes with intensive monocultures can limit these resources, thereby negatively impacting bee reproduction and population stability (Potts et al. 2016). Therefore, it is critical to understand how different materials and cavity dimensions impact nesting success across locations.

Despite these structures being increasingly used in agricultural landscapes, most research to date has focused on managed bee populations in temperate regions. In contrast, the spontaneous colonisation of trap nests by wild *Osmia* species in Mediterranean orchard systems, where climatic and ecological conditions differ substantially, is poorly understood. Furthermore, the effectiveness of newer materials, such as paper tubes, in Mediterranean orchards has not been systematically evaluated.

To address these questions, this study investigated how trap nests support the natural populations of *Osmia* bees in Mediterranean orchards. Specifically, we: (1) characterised the assemblage of *Osmia* species that naturally colonise trap nests; (2) compared the nesting success and the brood viability between two types of nesting material (paper tubes and pinewood blocks), and two cavity diameters (6 mm and 8 mm); and (3) examined how nest features and landscape composition influence nest occupation by the target species identified in objective 1. Addressing this knowledge gap is essential for understanding how artificial nests function in natural colonisation scenarios as well as for identifying candidate species for future conservation and pollination management initiatives.

Methods

Study site

The research was conducted across 14 orchards in Central Portugal in 2022 and 2023, consisting of six apple (*Malus domestica* (Borkh.) Borkh.), six pear (*Pyrus communis* L.), and two cherry (*Prunus avium* L.) orchards (Fig. 1). The cherry orchards were located in the Fundão region, which is characterised by a mix of forests and extensive agricultural land and has a Mediterranean climate with cool, rainy winters and hot, dry summers (Monteiro-Henriques et al. 2016). The apple and pear orchards were situated in the Oeste region, closer to the Portuguese coastline. This region is known for its diverse landscape, which includes various fruit and vegetable crops. It has a milder and more humid



Fig. 1 (A) Location of the study site; (B) Location of the orchards where the trap nests were placed in the Oeste and Fundão regions; (C) Trap nest with four different nesting blocks made from paper tubes and pine wood, with diameters of 6 mm and 8 mm

climate than the Fundão region due to the influence of the Atlantic Ocean (Monteiro-Henriques et al. 2016).

The studied orchards were primarily managed conventionally, with farmers using pesticides in accordance with Integrated Pest Management (IPM) guidelines and applying artificial fertilisers. No managed bee colonies (e.g., honeybee apiaries) were present within the orchards and no solitary bee species were artificially introduced or reared at the sites prior to the experiment. The sites were all at least 1.6 km apart, with an average orchard size of 1.52 ± 1.70 (SD) hectares. The surrounding landscapes typically consisted of nearby orchards, meadows, fallows, and rural-urban areas.

In the Oeste region, apple and pear trees usually started flowering in early to late April, with the full bloom lasting approximately two to three weeks depending on the weather that year. Pear trees generally started flowering one to two weeks before apple trees. By contrast, cherry orchards located in Fundão began flowering slightly earlier, from late March to early April.

Experimental design and data collection

In each orchard, the trap nests were installed one to two weeks before the crops reached the flowering stage. Each trap nest comprised four different nesting blocks: pine wood blocks containing 66 and 63 circular cavities measuring 6 mm and 8 mm respectively, and paper tubes with the same diameter containing 64 cavities (Fig. 1). On average, each block contained 64.8 ± 1.3 (SD) cavities, each measuring 16 ± 1 (SD) cm in length. The paper tubes were specifically designed by Black System Company for *Osmia* bees. They were lighter and thinner than standard paper straws and had a protective metal sheet on the exterior to prevent kleptoparasitic wasps from entering. The tubes were mounted on a wooden support structure using food-grade glue, with one side closed. The pine wood blocks were drilled and sanded to ensure smooth cavity walls and to prevent splinters that could harm the bees. These blocks were housed in a wooden trap nest structure to protect them from the rain and secure all the blocks together.

The cavity diameter was chosen based on prior local observations and communications (C. Reis, pers. comm., 2020; R. Carvalho, pers. comm., 2021). Although *O. cornuta* is a recognised orchard pollinator, it was absent or present at very low frequencies in the studied orchards. As such, it was not specifically targeted, given that this species typically prefers wider cavity diameters.

Trap nests were installed on wooden poles approximately 50 cm above the ground, oriented towards the south or east to maximise sun exposure (Yoon et al. 2015; MacIvor 2017) and were also placed primarily along orchard boundaries.

At one site (PR00) this was not feasible during the first year, so the trap nest was installed within the orchard, next to a patch of herbaceous vegetation. Between early and mid-September, all trap nests were collected from the field to allow natural levels of parasitism and predation to occur, thus reflecting the conditions experienced by unmanaged nests. After collection, the trap nests were stored in a cool, dark environment until late November, when all cavities were opened for detailed examination.

We recorded whether each cavity was successfully occupied (i.e., contained at least one brood cell). In addition, we obtained the total number of viable brood cells (pre-winter), based on visual confirmation of healthy cocoons. Bee species were identified by their cocoons when possible; otherwise, identification occurred at hatching. Several features of the trap nests were recorded for each location, including the nest orientation (i.e. the direction it was facing), whether it was overshadowed (1 if covered by a tree, 0 if not), a qualitative assessment of the presence of arachnids (0=none, 1=low to medium, and 2=high), the type of orchard (pear, apple, or cherry), the placement date and year (2022 or 2023), and the orchard area (ha).

Statistical analysis

The statistical analyses focused on early-season *Osmia* species that could potentially pollinate orchards. To ensure analytical robustness, species exhibiting oligolectic foraging behaviour, as well as species and orchard types that failed to meet the minimum thresholds for nest occurrence, were excluded. All analyses were conducted using R software (version 4.3.2; R Development Core Team, 2020).

Nesting rates and brood viability were recorded for each type of nesting material and diameter across the 14 orchards. Nesting success was assessed at the cavity level and defined as the presence (1) or absence (0) of brood cells. To evaluate the separate effects of material and diameter on nesting success and brood viability, we fitted generalised linear mixed-effects models (GLMMs) for each species, using the *glmmTMB* package with binomial error distribution and a logit link. The fixed effects included cavity diameter (6 mm vs. 8 mm) and nesting material (pine wood vs. paper tubes), while trap nest location was included as a random effect to account for spatial dependency. Model residuals were validated using the *DHARMA* package, which confirmed that there were no issues with overdispersion or zero-inflation.

A second model was performed to examine the influence of landscape composition, orchard features and nest characteristics on nesting success. For each location, the landscape composition was characterised within a 500 m buffer zone around the trap nests, based on the typical maximum flight range of *Osmia* bees (MacIvor and Packer 2015).

The surrounding landscape was characterised using the CORINE Land Cover (2018) database (Online Resource 1). All analyses were conducted using QGIS (version 3.4.13, QGIS Development Team, 2018).

First, a correlation analysis was performed to assess potential multicollinearity among the variables. We then constructed species-specific Generalized Linear Mixed Models (GLMMs) with a beta-binomial error distribution and logit link function (function *glmmTMB*, package *glmmTMB*), to account for overdispersion in the nesting data. The model included trap nest characteristics (e.g. orchard area, material, diameter, nest orientation, shade, year, and orchard type) and landscape variables (CORINE land use area within a 500 m buffer, number of different land use types within the buffer, and orchard area) as fixed effects. Trap nest location (*ID_nest*) was included as a random effect to account for unobserved heterogeneity. Model selection was performed using a stepwise approach, with the final model being chosen based on the lowest Akaike Information Criterion (AIC). Model residuals were validated using the *DHARMA* package.

Results

Trap nest occupancy and species composition

A total of 14 species of nesting bee were recorded across the three orchard types (Online Resource 2). However, only three of these species are considered to be orchard pollinators: *Osmia bicornis*, *Osmia caerulea* (Linnaeus, 1758),

and *Osmia cornuta*. *Osmia caerulea* was the dominant species, accounting for approximately 81% of all nests across all orchard types, followed by *Osmia bicornis* (15%) and *Osmia cornuta* (4%) (Online Resource 2). Notably, *Osmia bicornis* was absent from cherry orchards throughout the study. In 2022, two trap nests showed no nesting activity by any of these three species (Table 1).

Across the 14 trap nests, a total of 537 nesting cavities were recorded, giving an average nesting rate of approximately 8% per trap nest per year. However, nesting success varied significantly depending on orchard type, bee species, nest diameter and nest material. Cherry orchards had the highest nesting rate at 21.8% per trap nest, while apple and pear orchards had much lower rates, at 4.9% and 5.2%, respectively. Despite accounting for only one-third of the total number of nesting cavities, cherry orchards represented 42% (224 nests) of all nests, with apple orchards accounting for 28% (152 nests) and pear orchards for 30% (161 nests) (Fig. 2 and Online Resource 2). Most nesting activity occurred in 6 mm cavities, accounting for 70% (377 nests) of all occupied nesting cavities, compared to 30% (160 nests) in 8 mm cavities. Similarly, bees showed a marked preference for paper tubes, with 78% (419 nests) being established in this material, compared to 22% (118 nests) in pine wood blocks.

A notable phenomenon observed during the study was the creation of “false nests”, where bees capped the entrances to the nests without any visible nesting activity inside. Furthermore, trap nests were inhabited by various non-bee taxa, including wasps, flies, and mites (Online Resource 2).

Table 1 Nesting activity and reproductive success of *Osmia* bees in trap nests installed in Cherry (CH), Apple (AP), and Pear (PR) orchards in 2022 and 2023. For each trap nest (Nest ID), the following variables are reported for each year: (i) the percentage of occupied cavities (% Nesting); (ii) the total number of viable brood cells, defined as those that developed successfully without signs of mortality or parasitism; and (iii) brood viability, calculated as the proportion of viable brood cells relative to the total number of brood cells. Trap nests with no activity are indicated as 0, and missing data are indicated as N/A

Orchard type	Nest ID	2022			2023		
		% Nesting	Total viable brood cells	% Brood viability	% Nesting	Total viable brood cells	% Brood viability
Cherry	CF00	23	343	73	25	83	27
	CF01	33	260	68	7	30	38
Apple	AP01	7	35	53	8	78	72
	AP04	10	61	82	12	59	65
	AP08	2	21	95	7	23	32
	AP01	2	6	100	7	73	73
	AP02	1	8	89	3	16	67
	AP07	0	0	0	0	0	0
Pear	PR00	0	0	0	2	25	0
	PR06	4	34	87	5	35	35
	PR09	11	91	82	N/A	N/A	N/A
	PR13	2	13	57	2	20	74
	PR14	1	6	86	5	26	70
	PR17	17	91	89	1	2	100
	PR20	N/A	N/A	N/A	14	30	15

Fig. 2 Number of occupied nest-ing cavities (\log_{10} -transformed) shown per trap nest, categorised by orchard type and nesting material. The white boxplots represent 6 mm cavities and while the grey boxplots represent 8 mm cavities. The y-axis has been \log_{10} -transformed to reduce visual skewness caused by the prevalence of low or zero nesting counts. Only trap nests with at least one occupied cavity are shown. Each orchard type included six trap nests for apple ($n=152$ nests) and pear ($n=161$ nests), and two for cherry ($n=224$ nests)

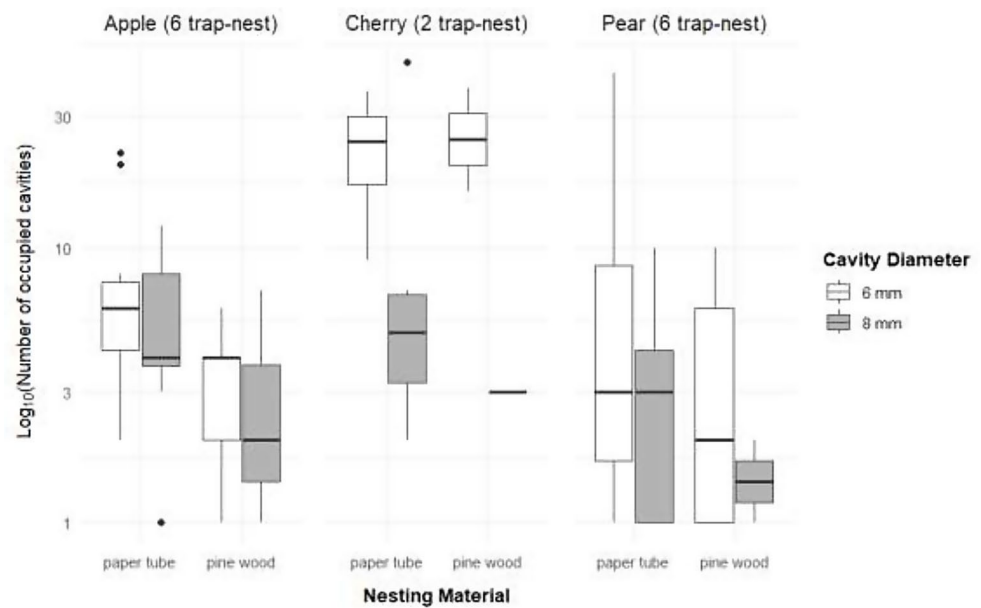
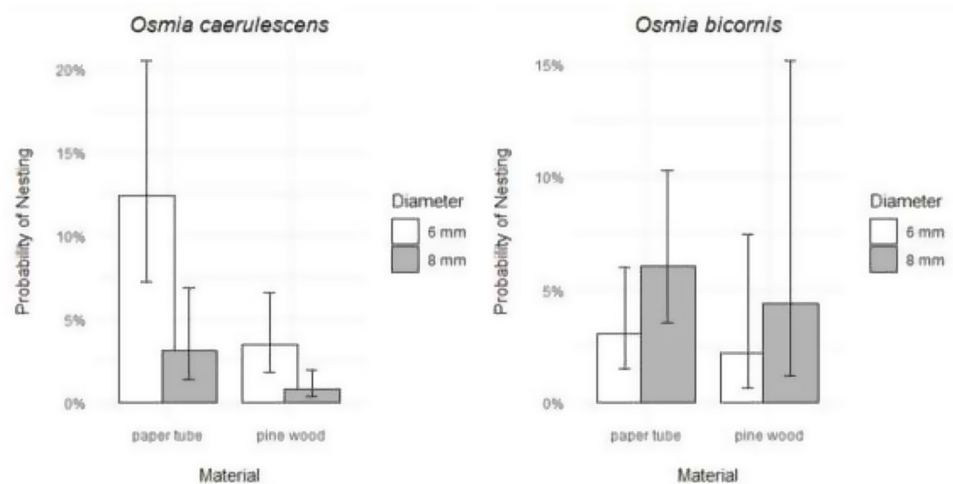


Fig. 3 Predicted probability of nesting for *Osmia caerulescens* (left) and *Osmia bicornis* (right) across two nesting materials (paper tube and pine wood) and two cavity diameters (6 mm and 8 mm). These predictions are based on zero-inflated binomial GLMMs fitted separately for each species and represent the model-estimated probability of cavity occupation with 95% confidence intervals



Nesting preferences and brood viability of target *Osmia* species in apple and pear orchards

The analyses of nesting preferences focused on *Osmia caerulescens* and *O. bicornis* in apple and pear orchards. *Osmia cornuta* was excluded from all models due to its low abundance (only 23 nests were found over two years). Cherry orchards were also excluded from further analysis, as only two trap nests were installed at these sites, and no *Osmia bicornis* specimens were recorded there throughout the study.

In both apple and pear orchards, the vast majority of *O. caerulescens* nests were found in 6 mm cavities (91% and 90%, respectively). Similarly, paper tubes accounted for a higher proportion of nests (nearly 80%) in both orchards, whereas pine wood accounted for just 20% of nest occupancy (Online Resource 2). The binomial GLMM supported

these observations. Nesting success was significantly lower in pine wood than in paper tubes (Estimate = -1.38 ± 0.19 SE, $p < 0.001$) in 8 mm cavities than in 6 mm (Estimate = -1.47 ± 0.31 SE, $p < 0.001$) (Fig. 3).

In terms of reproductive success, the brood viability of *O. caerulescens* was higher in paper tubes (63%) than in pine wood (46%), and in 8 mm cavities (62%) than in 6 mm (57%) (Table 1). Although no significant effects were detected, the effect of nest material approached significance, with pine wood tending to reduce brood viability (Estimate = -0.261 ± 0.14 SE, $p = 0.062$). Cavity diameter had no detectable effect (Estimate = 0.168 ± 0.27 SE, $p = 0.52$) (Online Resource 2).

By contrast, *O. bicornis* mainly nested in 8 mm cavities. In apple orchards, 78% of nests were found in 8 mm cavities, compared to 22% in 6 mm cavities. In pear orchards, this proportion was more balanced, at 56% and

Table 2 Results of generalized linear mixed-effects models (GLMM) that assessed the effect of trap nest features, landscape complexity and areas of land use type areas (within a 500 m buffer) on the nesting success of *Osmia* spp. The full model was tested, and the model statistics are presented as model estimates (ES), standard errors (SE), z-scores (Z) and p-values

Species	Fixed effects	ES	SE	Z	p-values
<i>Osmia caerulescens</i>	Intercept	-9.07	1.74	-5.20	<0.001
	Year – 2023	0.52	0.38	1.37	0.17
	Diameter – 8 mm	-1.85	0.42	-4.40	<0.001
	Material – Paper tube	0.75	0.35	2.14	0.03
	Number of Land-use types	1.13	0.37	3.08	0.002
	Discontinuous urban fabric	-5.81	3.30	-1.76	0.08
	Non-irrigated arable land	6.06	1.48	4.09	<0.001
	Complex cultivation patterns	2.22	1.47	1.50	0.13
	Fruit trees and berry plantations	2.51	0.95	2.63	0.009
<i>Osmia bicornis</i>	Intercept	-7.83	0.97	-8.10	<0.001
	Orchard type - Pear	-2.13	0.54	-3.94	<0.001
	Material - Paper tube	2.12	0.62	3.39	<0.001
	Discontinuous urban fabric	7.95	3.61	2.20	0.03
	Non-irrigated arable land	3.95	1.86	2.12	0.03
	Fruit trees and berry plantations	5.35	1.27	4.21	<0.001

44% respectively (Table 1). Regarding nesting material, *O. bicornis* showed a strong preference for paper tubes in both orchard types: 83% in apple orchards and 89% in pear orchards (Table 1). The binomial GLMM model revealed a significant positive effect of 8 mm cavities on nesting probability (Estimate = 0.72 ± 0.30 SE, $p = 0.014$), though no effect of material was detected (Estimate = -0.34 ± 0.63 SE, $p = 0.592$) (Fig. 2B).

Brood viability in *O. bicornis* remained stable across different nest materials and cavity diameters, with values of 66% in paper tubes, 71% in pine wood, and 68% and 70% in 8 mm and 6 mm cavities respectively (Online Resource 2). The statistical model corroborated these patterns, finding no significant effect of nest material (Estimate = 0.07 ± 0.22 SE, $p = 0.746$) or cavity diameter (Estimate = -0.01 ± 0.19 SE, $p = 0.942$) on reproductive success.

Influence of landscape complexity and trap nest features on nesting success in pear and apple orchards

Nesting success was significantly influenced by several trap nest features and landscape characteristics (Table 2). For *O. caerulescens* the model showed lower nesting success in 8 mm cavities than in 6 mm (Estimate = -1.85 ± 0.42 SE, $p < 0.001$), as well as a moderate positive effect of paper tubes compared to pine wood blocks (Estimate = 0.75 ± 0.35 SE, $p = 0.032$). Among the landscape-level predictors, nesting success increased significantly with greater land-use diversity within 500 m (Estimate = 1.13 ± 0.37 SE, $p = 0.002$). The presence of “non-irrigated arable land” and “fruit trees and berry plantations” also had significant positive effects (Estimate = 6.06 ± 1.48 SE, $p < 0.001$; and Estimate = 2.51 ± 0.95 SE, $p = 0.009$, respectively). A marginal negative effect of discontinuous urban fabric was observed but this did not reach significant levels (Estimate = -5.81 ± 3.30 SE, $p = 0.078$).

For *O. bicornis*, the final model retained orchard type, trap nest material, and three landscape variables (Table 2 and Online Resource 4). Nesting success was significantly higher in apple orchards than in pear orchards (Estimate = -2.13 ± 0.54 SE, $p < 0.001$), and in paper tubes than in pine wood blocks (Estimate = 2.12 ± 0.62 SE, $p < 0.001$). At the landscape scale, *O. bicornis* also responded positively to the percentage of non-irrigated arable land (Estimate = 3.95 ± 1.86 SE, $p = 0.034$), fruit trees and berry plantations; (Estimate = 5.35 ± 1.27 SE, $p < 0.001$), and discontinuous urban fabric (CLC 112; Estimate = 7.95 ± 3.61 SE, $p = 0.028$).

Discussion

This study evaluated the spontaneous nesting behaviour of wild *Osmia* species in Mediterranean orchards and investigated how nest characteristics and landscape context influence nesting success. *O. caerulescens* was the most abundant species in our study assemblage across all orchard types, followed by *O. bicornis*, while *O. cornuta* was rarely detected. These results differ from those observed in temperate regions of Central and Northern Europe, where *O. bicornis* or *O. cornuta* typically dominate trap nest assemblages (Kratschmer et al. 2020; Bihaly et al. 2021; Eeraerts et al. 2022). However, they align with emerging evidence from Mediterranean systems, where *O. caerulescens* appears to be a dominant trap nesting species, as reported recently in cherry orchards in central Spain (Tobajas et al. 2022). The ecological success of *O. caerulescens* in Mediterranean environments may be linked to its bivoltine life cycle in

these climates (Westrich 1990; Sedivy et al. 2013), which enables it to exploit early-season floral resources. While its activity period is generally described as extending from May to September (Tasei and Piccart 1972; Vicens et al. 1993), we observed males emerging from cocoons in early March and females in mid-March. This suggests the possibility of phenological shifts that could enhance synchronisation with orchard bloom. While our sampling design accounted for crop type, we did not directly evaluate nesting activity or floral visitation during the peak bloom of each orchard. Future studies should quantify species-specific nesting and foraging activity in relation to the flowering phenology of each crop, to better evaluate temporal mismatches that may affect pollination services. As expected, *O. cornuta* was recorded only at low frequencies, as our trap nest design did not include suitable cavity diameters (Bosch and Kemp 2002). Nevertheless, the presence of this species in our samples suggests that it could also be supported in these orchard systems if suitable nesting conditions were provided.

Nesting rates varied across orchard types, with cherry orchards supporting higher nesting rates than apple or pear orchards. This pattern is likely due to the greater structural heterogeneity and the higher proportion of semi-natural habitats in the Fundão landscape (Hamroud et al. 2023; Hyjazie and Forrest 2024), which extends the availability of flowers beyond the peak bloom of the crops. These results are consistent with studies showing that structurally diverse landscapes promote higher solitary bee abundance (Hamroud et al. 2023; Tobajas et al. 2022; Bottero et al. 2023; Hyjazie and Forrest 2024). The relatively low nesting rates observed in apple and pear orchards, compared to other studies (Yoon et al. 2015; Bihaly et al. 2021; Rahimi et al. 2021; Gilpin et al. 2022; Hyjazie and Forrest 2024), may be partly explained by the trap nest design used in this study (e.g. the number of cavities per nest or the type of material used). Nesting success was higher in the second year of the study. This may be linked to the trap nest being placed earlier, approximately 10 days earlier than in the first year. This improved the synchronisation of the emergence of the *Osmia* species, particularly *O. bicornis*, which tends to emerge earlier than *O. caerulea* (Bosch and Kemp 2002; Radmacher and Strohm 2010). This highlights the importance of installation timing in maximising nest colonisation. A variation of 10–14 days can be critical in early spring, when weather fluctuations can accelerate or delay bee emergence (Slominski and Burke 2021).

The occurrence of capped cavities without brood cells (false nests) is poorly documented, but it is thought to be a strategy employed by females to confuse parasites or predators (Henry et al. 2023). This behaviour may be particularly important when nesting resources are scarce, as it may reduce the likelihood of viable brood cells being predated.

To better understand species-specific nesting preferences, the following analyses focused on *O. bicornis* and *O. caerulea*. These two species were chosen as they had a higher nest occupancy rate. Initially nesting preferences were assessed based solely on cavity material and diameter, without considering nest or landscape-level variables. *O. caerulea* showed a clear preference for 6 mm cavities and paper tubes, whereas *O. bicornis* showed a significant preference only for 8 mm cavities, with nest material having no significant effect on this species. These results are consistent with those of previous studies reporting species-specific preferences for cavity diameter and material (Sedivy and Dorn 2013; Eeraerts et al. 2022; Zadjel et al. 2024) and align with morphological differences between these species. Although the material effect was not statistically significant for *O. bicornis*, a higher proportion of nests were still observed in paper tubes. This preference may be attributed to the structural advantages of paper tubes, which provide a consistent and secure nesting environment (Joshi et al. 2020; Eeraerts et al. 2022; Zadjel et al. 2024). Unlike pine wood blocks, which can develop cracks and gaps over time due to temperature fluctuations, potentially compromising brood cell sealing, paper tubes offer a smooth, fully enclosed surface (Eeraerts 2020; Joshi et al. 2020).

Examining reproductive success, the statistical models showed that brood viability did not differ significantly between materials or diameters in the statistical models. However, there was a trend towards significance in nest material, with pine wood tending to reduce reproductive success in *O. caerulea*. This species also exhibited lower overall viability, particularly in pine wood blocks (43%), whereas *O. bicornis* maintained higher viability consistently across substrates. Interestingly, viability in paper tubes was similar between species. These differences may be related to cocoon structure and nest architecture. *O. caerulea* produces thinner cocoons and uses chewed leaves to partition brood cells, which may offer less protection against desiccation or natural enemies, especially in rough or porous materials such as pine wood (Bosch and Kemp 2002; Westrich 1990). In contrast, *O. bicornis* constructs robust mud partitions and thicker, more resilient cocoons (Bosch et al. 2001; Sedivy and Dorn 2013). These traits are likely to enhance physical protection and structural stability. Firstly, the differences between our results may be due to low nesting density (less than 10% occupancy), which likely increased exposure to parasites and predators by reducing the protective effect of having more nests occupied. Secondly, our trap nests were left outside throughout spring and summer, allowing them to accumulate temperature and humidity fluctuations that can promote fungal development and brood loss. In contrast, studies reporting higher viability often removed or refrigerated the cocoons shortly after nesting, thus mitigating

these environmental stressors (Bosch 1994; Fliszkiewicz et al. 2015; Zajdel et al. 2024). Published viability data for *O. caerulea* are scarce, though high offspring production has been noted in sun-exposed habitats (Tobajas et al. 2021; Polidori et al. 2024).

To further explore the drivers influencing nesting success, we developed multivariate GLMMs that incorporated not only cavity features (material and diameter) but also nest and landscape level variables. This approach enabled us to assess whether cavity-related patterns persisted when broader environmental factors were considered, and to identify additional variables influencing trap nest colonisation. The best models for *O. caerulea* and *O. bicornis* included predictors at the nest, orchard, and landscape scales. As with the cavity-only models, nesting success remained significantly higher in 6 mm cavities and in paper tubes for *O. caerulea*. However, for *O. bicornis*, cavity diameter was only significant when cavity traits were considered in isolation; it lost significance in the multivariate models, where nest material (paper tubes) emerged as the main predictor instead. This shift suggests that nesting success in *O. bicornis* may be more context dependent. Although paper tubes outperformed pine wood blocks in terms of colonisation and brood viability, our study only tested two nesting materials and two cavity diameters. This limits the generality of our conclusions. Other studies have shown high occupancy rates in natural substrates such as *Arundo canes* and *Phragmites* reeds, as well as in materials like MDF (Bosch and Kemp 2001; Wilkaniec and Giejdasz 2003; Staab et al. 2018). Some of these substrates may influence not only species preference but also the number of brood cells per cavity and long-term nest health (Eeraerts et al. 2022; Zajdel et al. 2024). Future research should expand the range of tested materials to better accommodate species with different body sizes and nesting strategies, including *O. cornuta*, which was rarely observed in this study. Furthermore, *O. bicornis* had significantly higher nesting success in apple orchards than in pear orchards. This suggests a phenological alignment between apple flowering and the foraging period of this species but may also reflect a behavioural avoidance for pear flowers. Pear nectar is known to be less attractive to pollinators due to its low sugar concentration (Smessaert et al. 2019). Previous studies have also highlighted *O. bicornis* as a successful pollinator and a frequent occupant of trap nests in apple-dominated landscapes, which supports this pattern (Gruber et al. 2011; Fliszkiewicz and Giejdasz 2023).

In addition to nest-level and orchard traits, landscape composition also emerged as an important driver of nesting success. Both species exhibited increased nesting success in response to fruit tree plantations and non-irrigated arable land. This finding is consistent with previous research

showing that orchard-rich landscapes provide cavity-nesting bees with abundant and phenologically synchronised floral resources (Gruber et al. 2011; Eeraerts et al. 2021; Magnin et al. 2025). The presence of multiple apple and pear cultivars in the surrounding landscape likely enhances floral continuity, creating favourable local conditions for *Osmia* spp. during the mass flowering period in spring (Dainese et al. 2018; Gilpin et al. 2022). Eeraerts et al. (2021) reported that nearly 90% of the offspring of *O. cornuta* and *O. bicornis* were produced during the peak bloom of fruit crops such as apples, pears, and sweet cherries, after which adult activity declined sharply. Given the short lifespan and limited foraging period of spring-flying *Osmia* bees, it is expected that most reproductive activity will occur during crop flowering, suggesting a strong phenological alignment between bee emergence and floral resource availability. Additionally, many of the orchards in the region area are managed using Integrated Pest and Pollinator Management (IPPM), incorporating practices such as inter-row grassing, which provides essential foraging resources, particularly in early spring (Campbell et al. 2017; Herz et al. 2019). In the Ooste region, arable land typically comprises abandoned or fallow orchards that remain undisturbed for several years before being replanted. These areas support rich herbaceous vegetation and offer sequential floral resources, which may be particularly valuable before and between orchard bloom periods (Dainese et al. 2018; Polidori et al. 2024; Tobajas et al. 2022). It is possible that *Osmia* individuals are recruited from these fallow areas as well as from other structurally complex elements of the landscape, such as hedgerows and small patches of semi-natural habitats (Bednarska et al. 2021; Bihaly et al. 2021; Bishop et al. 2023). On the other hand, this pattern may reflect 'desperation nesting' behaviour, whereby bees concentrate in trap nests due to a lack of suitable nesting or foraging habitats in the vicinity. The CORINE land cover classification does not account for habitat quality within these land-use categories. A more detailed characterisation of these habitats, particularly through floral resource mapping before, during, and after crop flowering, would be essential to improve our understanding of their actual contribution to solitary bee reproduction and persistence (Campbell et al. 2017; Eckerter et al. 2022; Ammann et al. 2024). The model for *O. caerulea* also showed that landscape heterogeneity positively influences nesting success. Various studies have shown that landscape heterogeneity enhances nesting and brood cell success in trap nests (Dainese et al. 2018; Staab et al. 2018; Tobajas et al. 2022; Polidori et al. 2024). Finally, discontinuous urban fabric had a positive effect on *O. bicornis*, but a marginally negative effect on *O. caerulea*, suggesting differential responses to rural urbanisation. While *O. bicornis* is well documented as exploiting floral resources in urban and rural

environments (Fortel et al. 2014), *O. caerulea*, although also recorded in urban landscapes (MacIvor et al. 2015; Ascher and Pickering 2019), may be more sensitive to habitat fragmentation or may preferentially avoid such areas.

Conclusion

Our findings demonstrate that Mediterranean orchards can support populations of *Osmia caerulea* and *Osmia bicornis* in the early spring by providing artificial nesting substrates, especially in structurally diverse landscapes. While both species successfully colonised trap nests in orchards, the extent to which they contribute to effective crop pollination remains unclear, as this study did not assess flower visitation or pollination outcomes. Although our results highlight the relative effectiveness of paper tubes in attracting *Osmia* nests, this study only tested two substrate types. Previous studies have reported high acceptance of more naturalised materials, which may influence not only occupancy but also nest architecture and brood productivity. Therefore, the apparent advantage of paper tubes should not be interpreted as a universal recommendation without further comparative evaluation. Material performance is likely to be species and context dependent, and additional studies under region-specific conditions remain essential.

The restricted range of materials and cavity diameters, as well as the timing of nest installation may have excluded key species such as *O. cornuta*. Similarly, landscape-level interpretations should be approached with caution, given the limited variability in land use across sites and the potential inaccuracy of the CORINE classification in reflecting habitat quality. Future research should aim to establish a link between nesting success and pollination effectiveness by integrating nesting data with pollen load and visitation frequency assessments. Long-term monitoring will be necessary to evaluate whether nesting support results in stable or growing populations, particularly when combined with complementary habitat enhancements. Ultimately, it is crucial to understand whether and how wild *Osmia* populations can be scaled up to function as managed pollinators, without negatively impacting other wild bee species, in order to integrate them into sustainable orchard management strategies.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-025-00690-8>.

Acknowledgements We would like to express our sincere gratitude to all the farmers who participated in this project. Special thanks go to COTHN for facilitating the link between our team and the farmers, and for providing logistical support during our visits to the orchards. We would also like to thank Dr. Pedro Nicolau for his invaluable assistance with the statistical analysis, particularly with regard to the

GLMM models. Finally, we are grateful to the anonymous reviewers for their constructive comments and suggestions, which substantially improved the quality of this manuscript.

Author contributions MA, EF and MTR conceived and designed the research. MA and RC conducted the experiments. MA analysed the data, prepared the figures and tables, and drafted the initial manuscript. EF and MTR managed project administration and funding acquisition. All authors contributed to the writing, and have reviewed drafts, and approved the final version of this paper.

Funding Open access funding provided by FCT/FCCN (b-on). This research was supported by FCT/MCTES with financial support to CE3C (UIDB/00329/2025), CHANGE LA/P/0121/2020 (<https://doi.org/10.54499/LA/P/0121/2020>), CESAM (<https://doi.org/10.54499/UIDB/50017/2020>, <https://doi.org/10.54499/UDP/50017/2020>), LEAF (UIDB/AGR/04129/2020; <https://doi.org/10.54499/UIDB/04129/2020>), TERRA-LA (LA/P/0092/2020; <https://doi.org/10.54499/LA/P/0092/2020>), and FLOWer Lab (UIDB/04004/2020). Additionally, it was funded by FCT/MCTES through national funds and co-financed by FEDER under the scope of the PT2020 Partnership Agreement and Compete 2020. Funding was also provided by COTHN-CC through the PoliMax project (*Promoção e aumento da eficiência da Polinização entomófila em macieiras, pereiras e cerejeiras*) (PDR2020-101-031733). MA gratefully acknowledges FCT for the PhD grant (2020.08908.BD).

Data availability No datasets were generated or analysed during the current study.

Declarations

Ethics approval Not applicable.

Consent to participate All orchards were privately owned, and consent was obtained from all the farmers to place the nests in their orchards.

Consent for publication Not applicable, as this study does not involve human participants or sensitive data.

Competing interests The authors declare no competing interests.

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References

- Aizen MA, Harder LD (2009) The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Curr Biol* 19:915–918. <https://doi.org/10.1016/j.cub.2009.03.071>

- Aizen MA, Aguiar S, Biesmeijer JC et al (2019) Global agricultural productivity is threatened by increasing 407 pollinator dependence without a parallel increase in crop diversification. *Glob Chang Biol* 25:3516–3527. <https://doi.org/10.1111/gcb.14736>
- Ammann L, Bøsem-Baillo d A, Herzog F, Frey D, Entling MH, Albrecht M (2024) Spatio-temporal complementarity of floral resources sustains wild bee pollinators in agricultural landscapes. *Agric Ecosyst Environ* 359:108754. <https://doi.org/10.1016/j.agee.2023.108754>
- Ascher JS, Pickering J (2019) Discover life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Available at: https://www.discoverlife.org/mp/20q?guide=Apoidea_species (accessed 3 March 2025)
- Bednarska AJ, Mikołajczyk Ł, Ziółkowska E, Kocjan K, Wnęk A, Mokkapati JS, Teper D, Kaczyński P, Łozowicka B, Śliwińska R, Laskowski R (2021) Effects of agricultural landscape structure, insecticide residues, and pollen diversity on the life-history traits of the red Mason bee *Osmia bicornis*. *Sci Total Environ* 794:148672. <https://doi.org/10.1016/j.scitotenv.2021.151142>
- Belien T, Raymaekers S, Eraerts M et al (2021) Towards integrated pest and pollinator management in intensive Pear cultivation: A case study from Belgium. *Insects* 12:901. <https://doi.org/10.3390/insects12100901>
- Bihaly ÁD, Kovács-Hostyánszki A, Szalai M, Sárospataki M (2021) Nesting activity of cavity-nesting bees and wasps is lower in small-scale Apple orchards compared to nearby semi-natural habitats. *Agric Entomol* 23:49–58. <https://doi.org/10.1111/afe.12403>
- Bishop GA, Fijen TPM, Desposato BN et al (2023) Hedgerows have contrasting effects on pollinators and natural enemies and limited spillover effects on Apple production. *Agric Ecosyst Environ* 346:108364. <https://doi.org/10.1016/J.AGEE.2023.108364>
- Bosch J (1994) The nesting behaviour of the Mason bee *Osmia cornuta* (Latr.) with special reference to its pollinating potential (Hymenoptera: Megachilidae). *Apidologie* 25:84–93. <https://doi.org/10.1051/apido:19940109>
- Bosch J, Kemp WP (2001) How to manage the blue orchard bee as an orchard pollinator. Sustainable Agriculture Network, Beltsville, MD. Handbook Series Book 5
- Bosch J, Kemp WP (2002) Developing and Establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. *Bull Entomol Res* 92:3–16. <https://doi.org/10.1079/ber2001139>
- Bosch J, Kemp WP, Trostle GE (2006) Bee population returns and Cherry yields in an orchard pollinated with *Osmia lignaria* (Hymenoptera: Megachilidae). *J Econ Entomol* 99:408–413. <https://doi.org/10.1603/0022-0493-99.2.408>
- Bottero I, Dominik C, Schweiger O et al (2023) Impact of landscape configuration and composition on pollinator communities across different European biogeographic regions. *Front Ecol Evol* 11:1128228. <https://doi.org/10.3389/fevo.2023.1128228>
- Boyle NK, Artz DR, Lundin O, Reberg-Horton SC, Legrand C, Delfosse E, Ward KL (2020) Wildflower plantings promote blue orchard bee, *Osmia lignaria* (Hymenoptera: Megachilidae), reproduction in California almond orchards. *Ecol Evol* 10:3189–3199. <https://doi.org/10.1002/ece3.5952>
- Breeze TD, Vaissière BE, Bommarco R et al (2014) Agricultural policies exacerbate honeybee pollination service supply-demand mismatches across Europe. *PLoS ONE* 9(1): e82996. 441 <https://doi.org/10.1371/journal.pone.0082996>
- Campbell AJ, Wilby A, Sutton P, Wäckers FL (2017) Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider Apple orchards. *Agric Ecosyst Environ* 239:20–29. <https://doi.org/10.1016/j.agee.2017.01.005>
- Connelly H, Poveda K, Loeb G (2015) Landscape simplification decreases wild bee pollination services to strawberry. *Agric Ecosyst Environ* 211:51–56. <https://doi.org/10.1016/j.agee.2015.05.004>
- Dainese M, Riedinger V, Holzschuh A, Steffan-Dewenter I (2018) Managing trap-nesting bees as crop pollinators: Spatiotemporal effects of floral resources and antagonists. *J Appl Ecol* 55:195–204. <https://doi.org/10.1111/1365-2664.12930>
- Eckert PW, Albrecht M, Herzog F, Entling MH (2022) Floral resource distribution and fitness consequences for two solitary bee species in agricultural landscapes. *Basic Appl Ecol* 65:1–15. <https://doi.org/10.1016/j.baec.2022.09.005>
- Eeraerts M (2020) Cardboard nesting cavities May promote the development of *Osmia cornuta* and reduce infestation of kleptoparasitic mites. *J Appl Entomol* 144:751–754. <https://doi.org/10.1111/jen.12793>
- Eeraerts M, Borremans L, Smagghe G, Meeus I (2020a) A growers' perspective on crop pollination and measures to manage the pollination service of wild pollinators in sweet Cherry cultivation. *Insects* 11:1–8. <https://doi.org/10.3390/insects11060372>
- Eeraerts M, Vanderhaegen R, Smagghe G, Meeus I (2020b) Pollination efficiency and foraging behaviour of honey bees and non-Apis bees to sweet Cherry. *Agric Entomol* 22:75–82. <https://doi.org/10.1111/afe.12363>
- Eeraerts M, Piot N, Pisman M, Meeus I, Smagghe G (2021) Landscapes with high amounts of mass-flowering fruit crops reduce the reproduction of two solitary bees. *Basic Appl Ecol* 56:122–131. <https://doi.org/10.1016/j.baec.2021.07.005>
- Eeraerts M, Clymans R, Van Kerckvoorde V, Beliën T (2022) Nesting material, phenology and landscape complexity influence nesting success and parasite infestation of a trap-nesting bee. *Agric Ecosyst Environ* 332:107951. <https://doi.org/10.1016/j.agee.2022.107951>
- Fliszkiewicz M, Giejdasz K (2023) Effect of pollination by the *Osmia bicornis* (syn. *O. rufa*) bee on fruit set, seed set and yield in three Apple cultivars. *J Apic Sci* 67(2):125–134. <https://doi.org/10.2478/jas-2023-0011>
- Fliszkiewicz M, Kuśnierczak A, Szymaś B (2015) Reproduction of the red Mason solitary bee *Osmia rufa* (syn. *Osmia bicornis*) (Hymenoptera: Megachilidae) in various habitats. *Eur J Entomol* 112(1):100–105. <https://doi.org/10.14411/eje.2015.00>
- Fortel L, Henry M, Guilbaud L, Guirao AL, Kuhlmann M, Mouret H, Rollin O, Vaissière BE (2014) Decreasing abundance, increasing diversity and changing structure of the wild bee community (Hymenoptera: Anthophila) along an urbanization gradient. *PLoS ONE* 9(8):e104679. <https://doi.org/10.1371/journal.pone.0104679>
- Garibaldi LA, Carvalheiro LG, Leonhardt SD, Aizen MA, Blaauw BR, Isaacs R, Kuhlmann M, Kremen C, Morandin LA, Schepher J, Szentgyörgyi H (2014a) From research to action: enhancing crop yield through wild pollinators. *Front Ecol Environ* 12:439–447. <https://doi.org/10.1890/130330>
- Garibaldi LA, Steffan-Dewenter I, Winfree R et al (2014b) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339:1608–1611. <https://doi.org/10.1126/science.1230200>
- Garibaldi LA, Pérez-Méndez N, Garratt MPD, Gemmill-Herren B, Miguez FE, Dicks LV (2019) Policies for ecological intensification of crop production. *Trends Ecol Evol* 34:282–286. <https://doi.org/10.1016/j.tree.2019.01.003>
- Gérard M, Marshall L, Martinet B, Michez D (2021) Impact of landscape fragmentation and climate change on body size variation of bumblebees during the last century. *Ecography* 44:255–264. <https://doi.org/10.1111/ecog.05310>
- Gilpin A-M, Brettell LE, Cook JM, Power SA (2022) The use of trap-nests to support crop pollinators in agricultural areas. *Ecol Res* 37:768–779. <https://doi.org/10.1111/1440-1703.12348>

- Goulson D, Nicholls E, Botías C, Rotheray EL (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347:1255957. <https://doi.org/10.1126/science.1255957>
- Gruber B, Eckel K, Everaars J, Dormann FC (2011) On managing the red mason bee (*Osmia bicornis*) in apple orchards. *Apidologie* 42:564–576. <https://doi.org/10.1007/s13592-011-0059-z>
- Hallmann CA, Sorg M, Jongejans E, Siepel H, Hoffand N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, Goulson D, de Kroon H (2017) More than 75% decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE* 12:e0185809. <https://doi.org/10.1371/journal.pone.0185809>
- Hamroud L, Lhomme P, Christmann S et al (2023) Conserving wild bees for crop pollination: efficiency of bee hotels in Moroccan Cherry orchards (*Prunus avium*). *J Apic Res* 62:1123–1131. <https://doi.org/10.1080/00218839.2022.2046528>
- Henry M, Berrou PJ, Bourdon S, Guilbaud L, Vaissière BE (2023) Assessing concrete nest boxes for cavity-nesting bees. *Biodivers Conserv* 32(14):4679–4700. <https://doi.org/10.1007/s10531-023-02719-3>
- Herz A, Cahenzli F, Penvern S, Pfiffner L, Tasin M, Sigsgaard L (2019) Managing floral resources in Apple orchards for pest control: ideas, experiences and future directions. *Insects* 10:247. <https://doi.org/10.3390/insects10080247>
- Hyjazie BF, Forrest JRK (2024) Supplemental nesting habitat increases bee abundance in Apple orchards. *J Appl Ecol* 61:442–451. <https://doi.org/10.1111/1365-2664.14570>
- Joshi NK, Naithani K, Biddinger DJ (2020) Nest modification protects immature stages of the Japanese orchard bee (*Osmia cornifrons*) from invasion of a cleptoparasitic mite pest. *Insects* 11:65. <https://doi.org/10.3390/insects11010065>
- Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. *Proc R Soc B* 274:303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Klein AM, Boreux V, Fornoff F, Mupepele AC, Pufal G (2018) Relevance of wild and managed bees for human well-being. *Curr Opin Insect Sci* 26:82–88. <https://doi.org/10.1016/j.cois.2018.02.011>
- Kline C, Joshi NK (2020) Flower abundance and diversity drive wild bee pollinator services to commercial Apple orchards. *Insects* 11:341. <https://doi.org/10.3390/insects11060341>
- Kline O, Phan NT, Porras MF, Chavana J, Little CZ, Stemet L, Acharya RS, Biddinger DJ, Reddy GVP, Rajotte EG, Joshi NK (2023) Biology, genetic diversity, and conservation of wild bees in tree fruit orchards. *Biology* 12:31. <https://doi.org/10.3390/biology12010031>
- Koh I, Lonsdorf EV, Williams NM, Brittain C, Isaacs R, Gibbs J, Ricketts TH (2016) Modeling the status, trends, and impacts of wild bee abundance in the united States. *Proc Natl Acad Sci USA* 113:140–145. <https://doi.org/10.1073/pnas.1517685113>
- Kratschmer S, Petrović B, Curto M, Meimberg H, Pachinger B (2020) Pollen availability for the horned Mason bee (*Osmia cornuta*) in regions of different land use and landscape structures. *Ecol Entomol* 45:525–537. <https://doi.org/10.1111/een.12823>
- MacIvor JS (2017) Cavity-nest boxes for solitary bees: A century of design and research. *Apidologie* 48:311–327. <https://doi.org/10.1007/s13592-016-0477-z>
- MacIvor JS, Packer L (2015) Bee hotels as tools for native pollinator conservation: A premature verdict? *PLoS ONE* 10:e0122126. <https://doi.org/10.1371/journal.pone.0122126>
- Magnin L, Bianchi F, Hagenbucher S (2025) *Osmia cornuta* is a more suitable managed pollinator for Cherry and Apple orchards than *Osmia bicornis*. *J Appl Entomol* 0:1–12. <https://doi.org/10.1111/jen.13399>
- Mallinger RE, Gratton C (2015) Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop. *J Appl Ecol* 52:323–330. <https://doi.org/10.1111/1365-2664.12377>
- McKerchar M, Potts SG, Fountain MT, Garratt MPD (2020) The potential for wildflower interventions to enhance natural enemies and pollinators in commercial Apple orchards is limited by other management practices. *Agric Ecosyst Environ* 301:107034. <https://doi.org/10.1016/j.agee.2020.107034>
- Monteiro-Henriques T, Martins MJ, Cerdeira JO, Silva PC, Arsénio P, Silva Á, Bellu A, Costa JC (2016) Bioclimatological mapping tackling uncertainty propagation: application to mainland Portugal. *Int J Climatol* 36:400–411. <https://doi.org/10.1002/joc.4357>
- Pardo A, Borges PAV (2020) Worldwide importance of insect pollination in Apple orchards: A review. *Agric Ecosyst Environ* 293:106839. <https://doi.org/10.1016/j.agee.2020.106839>
- Pisman M, Eeraerts M, Ariza D et al (2022) Increased compositional heterogeneity of mass-flowering orchard crops does not promote wild bee abundance in orchards. *Agric Entomol* 24:8–17. <https://doi.org/10.1111/afe.12464>
- Polidori C, Rodrigo-Gómez S, Ronchetti F et al (2024) Sunny, hot and humid nesting locations with diverse vegetation benefit *Osmia* bees nearby almond orchards in a mediterranean area. *J Insect Conserv* 28:57–73. <https://doi.org/10.1007/s10841-023-00523-6>
- Potts SG, Imperatriz-Fonseca V, Ngo HT, Biesmeijer JC, Breeze TD, Dicks LV, Garibaldi LA, Hill R, Settele J, Vanbergen AJ (2016) Safeguarding pollinators and their values to human well-being. *Nature* 540:220–229. <https://doi.org/10.1038/nature20588>
- Prete R, Brown C, Polce C et al (2021) Large variability in response to projected climate and land-use changes among European bumblebee species. *Glob Chang Biol* 27:4530–4545. <https://doi.org/10.1111/gcb.15780>
- QGIS Development Team (2018) QGIS Geographic Information System (version 3.4.13). Open Source Geospatial Foundation Project. <https://download.qgis.org/downloads/>
- Radmacher S, Stroh E (2010) Factors affecting offspring body size in the solitary bee *Osmia bicornis* (Hymenoptera, Megachilidae). *Apidologie* 41:169–177. <https://doi.org/10.1051/apido/2009064>
- Rahimi E, Barghjelveh S, Dong P (2021) How effective are artificial nests in attracting bees? A review. *J Ecol Environ* 45:1–11. <https://doi.org/10.1186/s41610-021-00192-z>
- Reilly JR, Artz DR, Biddinger DJ et al (2020) Crop production in the USA is frequently limited by a lack of pollinators. *Proc R Soc B* 287:20200922. <https://doi.org/10.1098/rspb.2020.0922>
- Rollin O, Garibaldi LA (2019) Impacts of honeybee density on crop yield: A meta-analysis. *J Appl Ecol* 56:1152–1163. <https://doi.org/10.1111/1365-2664.13355>
- Rosas-Ramos N, Baños-Picón L, Tobajas E et al (2017) Tanto Los factores paisajísticos Como Los locales Influyen sobre Las estrategias de inversión parental de La Abeja solitaria *Osmia caerulea*. *J Apic Res* 56:1–12. <https://doi.org/10.1080/00218839.2017.1282079>
- Sedivy C, Dorn S (2013) Towards a sustainable management of bees of the subgenus *Osmia* (Megachilidae; *Osmia*) as fruit tree pollinators. *Apidologie* 45:88–105. <https://doi.org/10.1007/s13592>
- Seidelmann K, Bienesch A, Pröhl F (2016) The impact of nest tube dimensions on reproduction parameters in a cavity nesting solitary bee, *Osmia bicornis* (Hymenoptera: Megachilidae). *Apidologie* 47:114–122. <https://doi.org/10.1007/s13592-015-0380-z>
- Slominski AH, Burkle LA (2021) Asynchrony between solitary bee emergence and flower availability reduces flower visitation rate and May affect offspring size. *Basic Appl Ecol* 56:1–10. <https://doi.org/10.1016/j.baae.2021.08.003>
- Smessaert J, Honnay O, Keulemans W (2019) Monitoring pollinator activity in an Apple and Pear orchard, linked with the analysis of

- the nectar composition. *Acta Hort* 1231:59–66. <https://doi.org/10.17660/ActaHortic.2019.1231.11>
- Staab M, Pufal G, Tschamtke T, Klein AM (2018) Trap nests for bees and wasps to analyse trophic interactions in changing environments—A systematic overview and user guide. *Methods Ecol Evol* 9:2226–2239. <https://doi.org/10.1111/2041-210X.13070>
- Tasei JN, Piccart M (1972) Observations préliminaires Sur La biologie d'*Osmia* (*Chalcosmia*) *caerulescens* L. (Hymenoptera: Megachilidae), pollinisatrice de La luzerne (*Medicago sativa* L.). *Apidologie* 3:149–165. <https://doi.org/10.1051/apido:19720203>
- Tobajas E, Rosas-Ramos N, Asís JD et al (2021) Effects of hillside aspect, landscape features, and kleptoparasitism on the reproductive success of the solitary bee *Osmia caerulescens*. *Ecol Entomol* 46(3):541–551. <https://doi.org/10.1111/een.13000>
- Tobajas E, de Paz V, Rosas-Ramos N et al (2022) Pollen use by the solitary bee *Osmia caerulescens* in Cherry orchard agroecosystems in Spain. *J Apic Res* 61:486–495. <https://doi.org/10.1080/00218839.2022.2080952>
- Vicens N, Bosch J, Blas M (1993) Análisis de Los Nidos de Algunos Megachilidae nidificantes En Cavidades preestablecidas (Hymenoptera, Apoidea). *Orsis* 8:53–63
- Westrich P (1990) *Die Wildbienen Baden-Württembergs*, vol 2. Ulmer, Stuttgart
- Wilkaniec Z, Giejdasz K (2003) The red Mason bee (*Osmia Rufa* L.) as an effective pollinator of Apple trees. *J Apic Sci* 47:61–67
- Winfree R, Williams NM, Gaines H, Ascher JS, Kremen C (2008) Wild bee pollinators provide the majority of crop visitation across land-use gradients in new Jersey and pennsylvania, USA. *J Appl Ecol* 45:793–802. <https://doi.org/10.1111/j.1365-2664.2007.01418.x>
- Winfree R, Bartomeus I, Cariveau DP (2011) Native pollinators in anthropogenic habitats. *Annu Rev Ecol Evol Syst* 42:1–22. <https://doi.org/10.1146/annurev-ecolsys-102710-145042>
- Yoon HJ, Lee KY, Kim SY et al (2015) Effects of location, direction, altitude, and placement of trap nests on the rate of trap-nesting of *Osmia* solitary bees. *J Asia Pac Entomol* 18:695–700. <https://doi.org/10.1016/j.aspen.2015.08.004>
- Zajdel B, Borański M, Kucharska K, Gąbka J (2024) The population development of the red Mason bee, *Osmia bicornis* L., for different types of nesting materials. *Animals* 14:3600. <https://doi.org/10.3390/ani14243600>
- Zhang H, Huang J, Williams PH, Vaissière BE, Zhou Z, Guo J, An J (2015) Managed bumblebees outperform honeybees in increasing Peach fruit set in china: different limiting processes with different pollinators. *PLoS ONE* 10:e0121143. <https://doi.org/10.1371/journal.pone.0121143>

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