CICLO: XXXIV

New insights on the nesting biology of three solitary bees (*Megachile sculpturalis, Osmia bicornis, O. tricornis*: Megachilidae) and monitoring wild bee pollination in urban and rural gardens.

Sara Straffon Díaz

Docente guida: **Coordinatore del Ciclo:**

Prof. Marco Porporato   **Prof. Domenico Bosco**

ANNI

2018-2021

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Summary

Wild and managed bees (Hymenoptera, Apoidea) are part of the most important pollinator group and are very meaningful for the preservation of all ecosystems. Providing pollination services, they enable the production of fruits, seeds, fodder, and the conservation of natural habitats (Garibaldi et al., 2013; Goulson, 2003; Klein et al., 2007). Around 50 of these species are managed for diverse purposes and 12 specifically for crop pollination. Among these, solitary bees of the genera *Osmia* and *Megachile* (Megachilidae) are a broad group of cavity nesting species that includes important managed pollinators (Russo et al., 2021) and are known to be mostly generalists. As cavity nester bees, they can be investigated using trap nesting methods that can provide fundamental information about their nesting biology and foraging patterns. This research was finalized to improve knowledge on nesting interactions and populations parameters for three solitary bee species of ecological and economic interest. Thereafter, I explored different aspects of the monitoring of wild bees on gardens (IPBES, 2016).

In Chapter 1, I first addressed the interaction in artificial trap nests, installed in a semi-urban area of north-western Italy, between the first exotic bee in Europe, *Megachile sculpturalis*, and the co-nesting native bee *Osmia cornuta*. Second, I evaluated the performance of the exotic bee by means of the sex ratio, and I screened for the presence of natural enemies affecting its brood. The results showed that *M. sculpturalis* brood cells cohabited tunnels with the native *O. cornuta.* Given the exotic cells' position within tunnels and their resin-based material, exotic cells may block native bee emergence. Moreover, this study revealed a strong male-biased sex ratio, suggesting a suboptimal reproductive trend for the *M. sculpturalis* local population. These novel findings broaden the knowledge on solitary bee invasions.

In Chapter 2, I analysed the provisioning patterns of two of the most known European cavity-nesting bees that are considered important insect study models: *Osmia bicornis* and *Osmia tricornis*. As polylectic bees, they forage from multiple plant families for pollen provisions, although they can vary greatly in their local specialization when foraging for either a genus or a family of flowering plants. Several studies have shown that *Osmia* populations are capable of adapting their foraging strategy depending on the resource availability and the quality of main pollen sources (Radmacher & Strohm, 2010; Splitt et al., 2021). In this experiment I evaluated reproductive traits such as progeny weight and sex ratio as parameters indicating individual and population fitness, and I dealt with the hypothesis that pollen composition of provisions gathered by mothers is adjusted along their reproductive lifespan and influences development of their offspring.

In Chapter 3, I documented the relevance of undertaking monitoring activities in a systematic and collaborative way in private and public gardens and urban orchards. I collaborated with a broad research group aiming to create a standardized global database of pollinator-plant interactions that could be meaningful to further analysis on biodiversity patterns of wild bee communities.

INTRODUCTION

Pollination by wild bees in agriculture

The production of diverse and affordable agricultural crop species depends on pollination services provided by bees. There are 87 globally important commercial crop species that depend on insect pollination (Klein et al., 2007). Of the more than 20,000 bee species (Hymenoptera: Apoidea) described worldwide (Ascher & Pickering, 2011; Gonzalez et al., 2013; Michener, 2007), only a handful are managed commercially as crop pollinators. For many modern crops requiring an animal pollinator, pollination is now an essential ecosystem service which should be managed as intensively as other aspects of agriculture by bringing large numbers of commercial pollinators directly to the field where pollination is needed (James & Pitts-Singer, 2008).

Bees are considered one of the most effective insect pollinators. Many insects visit flowers to collect pollen as food and pollinate the flowers in the foraging process. Most flowers have nectar to attract pollinators as a mechanism that evolved from their mutualistic interaction (Brandenburg et al., 2009). Bees are particularly effective insect pollinators because they feed on both pollen and nectar almost exclusively and store them for feeding their offspring. Due to these particular food requirements, they visit many flowers of the same species during a single trip and have specialized hairy bodies to collect and transport pollen.

While honey bees are traditionally considered to be the most valuable pollinators (Free, 1993), they are not the most efficient pollinators for all crops. Non-*Apis* bees are often effective and sometimes superior pollinators, and contribute significantly to crop yield (Klein et al., 2003; Kremen et al., 2007). For example, for "Red Delicious" apples, flowers visited by *Osmia cornuta* (Latreille) were five times more likely to set fruit than honey bee-visited flowers, and resulting

fruits were larger when flowers were visited by *O. cornuta* (Vicens & Bosch, 2000). In other studies, *Osmia* have been found to be suitable as alternative pollinators of several fruit trees (Krunic et al., 1995; Pinzauti et al., 1997). Moreover, honeybees do not efficiently pollinate certain crop plants such as blueberries (*Vaccinium* spp.) or tomatoes and potatoes (*Lycopersicum* spp. and *Solanum* spp., respectively) because of their inability to buzz-pollinate. Furthermore, they are unsuitable to pollinate in greenhouses where they suffer disorientation and may behave aggressively towards working staff when disturbed (Sedivy & Dorn, 2014).

The extent of our reliance mainly on a single species (*Apis mellifera* (Linnaeus)), for the pollination service in agriculture, is risky, whether this pollinator is managed or not. Other wild pollinators can contribute to crop pollination in four ways. First, they can substitute for the services provided by managed pollinators, replacing them either fully or partially. Second, they can enhance the services provided by managed pollinators through behaviours that increase the effectiveness of the managed pollinator. Third, they can provide services to plants that are not efficiently pollinated by a managed pollinator. Fourth, they can enhance productivity in plants that self-pollinate and for which pollination is consequently rarely managed.

Pollination services are shaped by different drivers. Agriculture and urbanisation are important global drivers of biodiversity change, negatively impacting some species groups, while providing opportunities for others. Diverse land types within European cities can be very rich in native flowering plant species and there is also an increasing interest in the potential of (outdoor) urban agriculture in ensuring food security (Theodorou et al., 2020). Yet the impact of urbanisation on the pollination of wild and cultivated plants remains poorly known.

While pollinator numbers and diversity are in serious decline, the expansion of pollination-dependent crops has accelerated (Aizen et al., 2019) and with it, the global dependence on insect pollination services. In the absence of animal pollination, crop production would decrease by more than 90 per cent in 12 per cent of the leading global crops. Moreover, 28 per cent of the crops would lose between 40 and 90 per cent of production, whereas the 45 per cent of the crops would lose between 1 and 40 per cent (IPBES, 2016).

Strategies to support alternative bee pollinators

High pollinator diversity increases the chances that an effective pollinator is present and actively providing pollination at any given time and location. To protect pollinators in agricultural and urban settings, different strategies can be adopted, which can be divided according to the main driver they are focused. This study focused on three of the strategies highlighted in bold below (Table 1).

Monitoring managed alternative pollinators

Among the species that are manageable as commercial crop pollinators other than honey bees, there are several bumblebee species, *Bombus* spp. (Hymenoptera: Apidae), which are extensively managed for pollination of tomato and other greenhouse crops (Velthuis & Doorn, 2006) Cavity-nesting solitary species developed as crop pollinators include the alfalfa leafcutting bee, *Megachile rotundata* (Fabricius) (Hymenoptera: Megachilidae), mostly managed for alfalfa pollination (Bohart, n.d.; Hobbs, 1967; Stephen & Osgood, 1965) and several species of mason bees, *Osmia* spp. (Hymenoptera: Megachilidae), mostly managed for pollination of rosaceous fruit tree species including almond, peach, apricot, plum, cherry, apple and pear (Bosch, 1994; Bosch & Kemp, 2002; Felicioli et al., 2004; Ladurner et al., 2004; Maccagnani et al., 2003; Torchio, 1981).

Table 1. List of some strategies relating to pollinators conservation in agricultural and urban context (IPBES, 2016)

Main driver	Strategies	Scientific evidence
Land use and its changes	Manage or restore habitat patches to support pollinators	Increases diversity and abundance of pollinating insects WELL ESTABLISHED
Pollinator management	**Monitor and evaluate managed pollinators**	**Large-scale monitoring programs have been shown to effectively collect and synthesize information on threats to honey bees, allowing coordinated responses (WELL ESTABLISHED), but such programs remain untested in other pollinator species**
Land management	**Monitor and evaluate pollinators and pollination on farms and cities**	**Increases diversity and abundance of pollinating insects ESTABLISHED BUT INCOMPLETE**
Changes in land cover and spatial configuration	Increase connectivity of habitat patches	Some evidence that habitat connections help pollinator movement and gene flow ESTABLISHED BUT INCOMPLETE
Land management	Provide nesting resources	Benefits to pollinator abundance and species ESTABLISHED BUT INCOMPLETE Little evidence for pollination service INCONCLUSIVE
Invasive species	**Manage invasive species (plants, pests, predators or pollinators) that diminish pollinators or pollinator habitat**	**Case study evidence of some benefits to pollinator species, but eradication is difficult to achieve ESTABLISHED BUT INCOMPLETE**
Multiple, interacting threats	Targeted conservation of specific pollinator species or groups of species (includes ex situ conservation of threatened species, includes species of special cultural value)	Examples exist for a limited range of taxa ESTABLISHED BUT INCOMPLETE
Multiple, interacting threats	Targeted conservation of pollinators associated with specific plant species threatened by pollination deficit	One European example known, for dittany (*Dictamnus albus*) INCONCLUSIVE
Land use and its changes	Establish protected areas or improve the quality of existing ones (including protected areas of cultural value)	Protected areas host species diversity, but it is difficult to determine the impact of legislation in achieving protection WELL ESTABLISHED

Table 1. (*Continuation*)

Land use and its changes	Payment for ecosystem services	Ecosystems services payments have been established for other services (watershed protection, carbon sequestration) but no examples for pollination ESTABLISHED BUT INCOMPLETE
Land use and its changes	Maintain sacred and other culturally protected areas that support pollinators	Protected areas host species diversity, but few case studies ESTABLISHED BUT INCOMPLETE
All	Increase taxonomic expertise on pollinator groups (formal education/training) and technology to support discovery and identification	Significant training has been achieved in a number of countries WELL ESTABLISHED

Two ground-nesting solitary bees, the alkali bee, *Nomia melanderi* (Cockerell), and the greyhaired alfalfa bee, *Rhophitoides canus* (Eversmann) (both Hymenoptera: Halictidae), are used as alfalfa pollinators in western USA and eastern Europe, respectively (Batra, 1976; Berezin & Beiko, 2002; Cane, 2008).

To improve the potential performance of a pollinator on different crops there are several steps that should be developed starting with identification of pollination-limited crop, pollination efficacy and biology of the species that would provide the guidelines on the pollinator management system. Basic knowledge on the nesting behaviour of the candidate species is important at an early stage of the pollinator development process, to provide adequate nesting resources and quantify populations (Bosch & Kemp, 2002). However, the population dynamics of the species need to be well known, to determine which factors limit population growth and to establish sustainable healthy bee populations.

Nesting biology of solitary bees

Most cavity nesting bees have management potential because their nesting requirement are largely understood (Lee-Mäder et al., 2010). A solitary bee, such

as a leafcutter bee, mason bee, or wool carder bee, begins life as a laid egg that hatches and the larva starts to eat the mass of pollen and nectar provided by the mother, who the bee will never meet. The larva is not completely alone; he or she shares a nest (hollow twig or soil tunnel) with developing brothers and sisters. Each larva develops in separate compartments within the nest that the mother partitioned off using leaves, mud or sand. There may be many nests aggregated in one area, a feature that can be exploited to manage these bees as pollinators.

There are two main types of life cycles in solitary bees: univoltine (a typical 1-year life cycle) and bivoltine (two-generations per year). For univoltine solitary bees such as *Osmia* spp., after consuming their share of pollen, the larvae spin their cocoons and reach the prepupa stage before developing to adult bees inside the cocoons. Later they will enter diapause, passing through the rest of summer, fall, and winter as adults in a state of suspended animation, and complete the emergence development rapidly the following spring (Figure 1). In some cases, the bee may complete development to the adult stage the next year. In either case, after hatching as an adult, the bee mates right away, ideally with individuals from a different nest. The male dies soon after mating, and the female then provides the environment service of transferring pollen from the flowers that are blooming around her through her foraging. She uses the pollen to provision her own nest as the mother of the next generation. She has no help from other bees and will die before her offspring complete their development the next year. These pollinating bees should be spotted upon their emergence every spring or summer; the rest of the year they are dormant and quiet to the world. A simple way to widen the knowledge of these wild bees for improved management is by using observation nests. Such nests typically consist of a grooved nest board (with a series of dead-end tunnels grooved along one side).

In Europe, the most ubiquitous representatives of solitary bees are the mason bee species *Osmia bicornis* (Linnaeus) (syn. *Osmia rufa* Linnaeus) and *O. cornuta*.

These bee species live in similar environments but differ in phenology and time of emergence in the spring. These species are two of the four *Osmia* species most successfully managed and increasingly used for pollination services in agriculture (Bosch & Kemp, 2002; Krunić & Stanisavljević, 2006; Sedivy & Dorn, 2014).
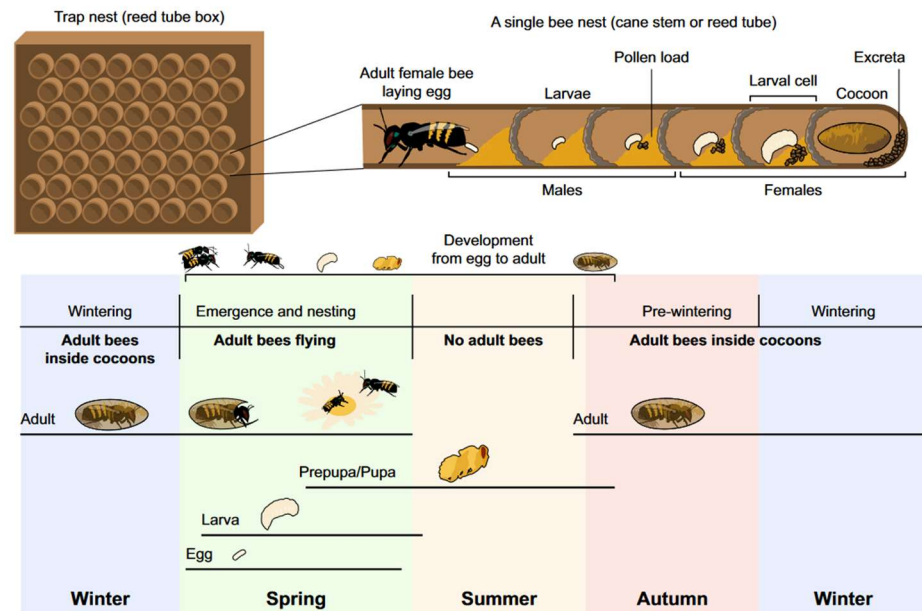
Figure 1. Life cycle of a solitary *Osmia* bee (Filipiak & Filipiak, 2020)

Bees often require specific nesting resources that can be enriched in a nature conservation strategy. For instance, for *O. bicornis,* the provision of nesting material (reeds) in habitat patches in an agricultural landscape led to a local population increase (Steffan-Dewenter & Schiele, 2008) and many other trials establish that appropriate artificial nesting shelters are used by a range of solitary bee species (Eeraerts et al., 2022; Felicioli et al., 2004, 2017; Krunić & Stanisavljević, 2006; Ladurner et al., 1999; Piano et al., 1998; Pinzauti et al., 1997; Seidelmann et al., 2016; von Königslöw et al., 2019).

Monitoring bee pollinators in urban areas

Habitat loss and fragmentation have pushed our wild pollinators to the margins of human civilization. Pollinators provide important pollination to urban landscapes as well. Given that urban areas are increasing globally (Seto et al., 2012), knowing how to managing urban green spaces to increase the local abundance of nectar-providing and pollen-providing flowering plants is crucial to increase pollinator diversity and abundance. Road verges, power lines, and railway banks in cities also have a large potential for supporting pollinators if managed appropriately to provide flowering and nesting resources (Felicioli et al., 2004, 2017; Foster et al., 2017; Majewska & Altizer, 2020; Plascencia & Philpott, 2017; Rollings & Goulson, 2019; Russo et al., 2013; Salisbury et al., 2015).

Researchers have also begun to study how landscape context influences the pollination provided by bees in cities. There are a great number of monitoring programs addressing the impact of urban land use on pollinator biodiversity and focusing on species richness (Hernandez et al., 2009; López-Uribe et al., 2015; MacIvor & Packer, 2016; Marín et al., 2020; Matteson et al., 2008; Millard et al., 2021; Prendergast et al., 2022; Theodorou et al., 2020). However, a lack of mechanistic understanding of the population processes causing biodiversity patterns limits advancement in urban-focused conservation (IPBES, 2016). One method to increase understanding on the effects of urbanisation on pollinators is involving urban residents together with scientific support. Urban residents are interested in conserving and enhancing pollinators by assisting with monitoring networks, construction of pollinator gardens and addition of artificial food and nesting resources. The small-scale actions accompanied by data collection are key elements to address effective conservation strategies involving community engagement (Dickinson et al., 2012; Flaminio et al., 2021; Levé et al., 2019).

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Invasive species: the case of solitary bees

One of the main conservation concerns related with pollinators is the negative impacts of managed non-native and invasive bee species on native wild bee species (Aizen et al., 2020). Many bee species have established outside their native ranges following accidental or intentional introductions (Goulson, 2003). For instance, cavity-nesting *Anthidium manicatum* (Linnaeus) and *Megachile* spp. were accidentally transported from Europe to North America through tranfer along of their nesting material, whereas other cavity-nesting *Osmia* have been transported intentionally in the same direction to improve pollination services (Aizen et al., 2020; Goulson, 2003). Invasive species can produce a complex array of impacts, and these often depend on context; the same introduced species can have minimal effects on native species and ecosystems in one region but can be devastating elsewhere (Russo, 2016; Russo et al., 2021). One of the mechanisms that produce negative impact across different families with cavity-nesting behaviour that has been documented is competition for nesting sites (e.g., between exotic *Megachile sculpturalis* (Smith) and *Xylocopa* sp. in America and Europe (Lanner et al., 2020a; Laport & Minckley, 2012a; Polidori & Sánchez-Fernández, 2020; Ruzzier, Menchetti, et al., 2020; Zandigiacomo & Grion, 2017).

Eradication of invasive species has proven difficult in most circumstances, with successful eradication most often occurring on islands (e.g. some invasive vertebrates and plants) where the management area is isolated, and re-invasion is less likely (Simberloff, 2013). In the case of an efficient pollinator invading new territories, concerns may increase when dealing with introduced plants associated with such invaders, that can promote invasive mutualism within the pollinator system (Abe et al., 2010). Because of this challenge, studies on the biology of the target organism are fundamental to the understanding and potential control of its spread (Simberloff et al., 2013).

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Chapter 1. Nesting, Sex Ratio and Natural Enemies of the Giant Resin Bee in Relation to Native Species in Europe

Sara Straffon-Díaz[1]*, Luca Carisio[1], Aulo Manino[1], Paolo Biella[2] and Marco Porporato[1]

*Corresponding author

Abstract: *Megachile sculpturalis* is the first exotic bee species in Europe. Its remarkably fast expansion across this continent is leading to a growing concern on the extent of negative impacts to the native fauna. To evaluate the interactions of exotic bees with local wild bees, we set up trap nests for above-ground nesting bees on a semi-urban area of north-western Italy. We aimed to investigate the interaction in artificial traps between the exotic and native wild bees and to assess offspring traits accounting for exotic bee fitness: progeny sex ratio and incidence of natural enemies. We found that the tunnels occupied by exotic bees were already cohabited by *Osmia cornuta*, and thus the cells of later nesting alien bees may block the native bee emergence for the next year. The progeny sex ratio of *M. sculpturalis* was strongly unbalanced toward males, indicating a temporary adverse population trend in the local invaded area. In addition, we documented the presence of three native natural enemies affecting the brood of the exotic bee. Our results bring out new insights on how *M. sculpturalis* indirectly competes with native species and on its performance in new locations.

Keywords: exotic bee; wild bees; *Megachile sculpturalis*; *Osmia cornuta*, bee invasion; nesting behavior; trap nest; competition; sex ratio; natural enemies

1.1 Introduction

[1] Department of Agricultural Forest and Food Sciences, University of Turin, Largo Paolo Braccini 2,n10095 Grugliasco (Turin), Italy; luca.carisio@unito.it (L.C.); aulo.manino@unito.it (A.M.); marco.porporato@unito.it (M.P
[2] Department of Biotechnology and Biosciences, University of Milano-Bicocca, Piazza della Scienza 2, 20126 Milano, Italy; paolo.biella@unimib.it

Introduced non-native bees (Hymenoptera Apoidea) can enhance pollination service, but they can also have detrimental effects on local ecosystems (Russo, 2016). Competition for floral resources or nesting sites, diseases transmission and changes in the pollination network are the mechanisms that have been deemed responsible for impacts directly on native bees (Goulson, 2003) and indirectly on plant communities (Rasmussen et al., 2012).

Megachile sculpturalis Smith, 1853, native from eastern Asia (China, Korea, Japan), is the first unintentionally introduced bee species in Europe, and it showed a remarkably fast spread across this continent. Since 2008, it expanded from southern France (Vereecken & Barbier, 2009) towards eastern Europe (Guariento E et al., 2019; Kovács, 2015; Lanner et al., 2020b; Le Féon et al., 2018; Quaranta et al., 2014; Westrich, 2015), reaching the Crimea peninsula in 2018 (Ivanov & Fateryga, 2019) and westwards eastern Spain (Aguado et al., 2018; Ortiz-Sánchez & varro, J.F., Taeger, 2019). Moreover, according to an evaluation of suitable climatic areas, *M. sculpturalis* is predicted to keep on spreading in most of Europe (Polidori & Sánchez-Fernández, 2020). Similarly, this species had rapidly colonized the entire eastern half of the USA since its arrival in 1994 (Hinojosa-Díaz, 2008; Hinojosa-Díaz, I. et al., 2005).

The fast spread of *M. sculpturalis* has been linked to some characteristics: the likely wide flight range according to its large body size (18–39 mm in length) (Greenleaf et al., 2007; Parys et al., 2015), the passive human-mediated dispersion via traded goods (Ruzzier, Ruzzier, et al., 2020), and the wide diet spectrum that includes different flowering plants, such as nectar and pollen sources (polylectic diet) (Andrieu-Ponel et al., 2018; Le Féon et al., 2018; Quaranta et al., 2014). In parallel to these aspects, *M. sculpturalis* is well-adapted to colonize anthropogenic environments, since it has a strong preference for ornamental plant pollen (Aguado et al., 2018; Guariento E et al., 2019), and it has an opportunistic nesting behavior, as it uses a diversity of pre-existing above-ground cavities regardless of their natural or human origin (Ivanov & Fateryga,

2019). Despite the great expansion of *M. sculpturalis*, the species has also displayed a male-biased sex ratio (Geslin et al., 2020). This trait is usually associated with a poor reproductive potential (Rosas-Ramos et al., 2017), and it could be a response to disadvantageous conditions due to eroded genetic diversity, resources shortage, inadequate climatic conditions or parasite pressure (Torchio & Tepedino, 1980a; Bosch & Vicens, 2005; Ulbrich & Seidelmann, 2001; Fitch et al., 2019; Collet et al., 2016). Therefore, whether the unbalanced sex ratio is a low fitness response or a generalized trait is still to be unveiled.

M. sculpturalis is a competitor for nesting resources against some native Apoidea species. In fact, the exotic bee has been found to evict pre-existing nesting sites of *Osmia* and *Xylocopa* (Lanner et al., 2020b; Laport & Minckley, 2012b; Parys et al., 2015; Zandigiacomo & Grion, 2017). Such an antagonistic nesting trait is likely to affect other above-ground nesting species that need a similar nesting substrate (holes in logs, stems, reeds, wooden trap nests) and similar cavity diameter (8–12 mm) (Geslin et al., 2020; Quaranta et al., 2014). A previous study has pointed out that the eviction mechanism may be among the reasons for the negative correlation seen between native bees and the exotic bee in an urban area in south France (Geslin et al., 2020). Nevertheless, giant resin bee nesting biology has not yet been widely studied, and besides the eviction mechanism, other direct or indirect interactions may be involved in the competition for nesting resources. The competition mechanisms with native bees are particularly important aspects for assessing the hypothesis that *M. sculpturalis* could harm native wild bees in Europe, and novel information on its behavior are essential to have a better understanding of its potential negative impacts.

The host-parasite system is among the factors facilitating the success of an invasion (Dunn, 2009). Parasites might mediate the invasion of an introduced species by modifying native host-parasites relationships (Parker et al., 2013a). To our knowledge, parasites and natural enemies of *M. sculpturalis* in either its home range or new locations have never been studied.

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This study provides new insights on traits linked to *M. sculpturalis* fitness in the new colonized area in Italy where it has been present since 2009 (Quaranta et al., 2014), and it adds novel evidence of likely negative effects of this exotic bee on native bee species. Specifically, our aims were: (1) to evaluate the interaction in artificial trap nests, located in Italian study areas, between native bees and the alien bee, (2) to explore the offspring progeny weight and sex ratio as parameters indicating species fitness, also in relation to the sex ratio detected for *M. sculpturalis* populations in the native and colonized areas, and (3) to provide the first report on natural enemies affecting the *M. sculpturalis* brood.

1.2 Materials and Methods

2.2.1 Study area and Study Organism

M. sculpturalis is a univoltine and protandric species, whose males emerge earlier than females (Lanner et al., 2020b). According to several reports, its nesting season starts in late June to early July and generally ends in mid-September (Hinojosa-Díaz, 2008; Quaranta et al., 2014). Like most Megachilidae species, it exhibits a sexual size dimorphism in which females are larger than males. This difference is also evident enough in brood cell sizes to allow preliminary gender recognition (Figure 1c). *M. sculpturalis*, like most solitary bees, has a high control over the size and sex of its offspring (Rosas-Ramos et al., 2017). It is a precavity nester bee, unable to excavate its own cavities and thus depending on the availability of suitable nesting places (Torchio & Tepedino, 1980a). Brood cells and nest closures are created using a mixture of wood fibers, leaf fragments, clay and resin (Michener, 2007) (Figure 1a 1b and 1c).

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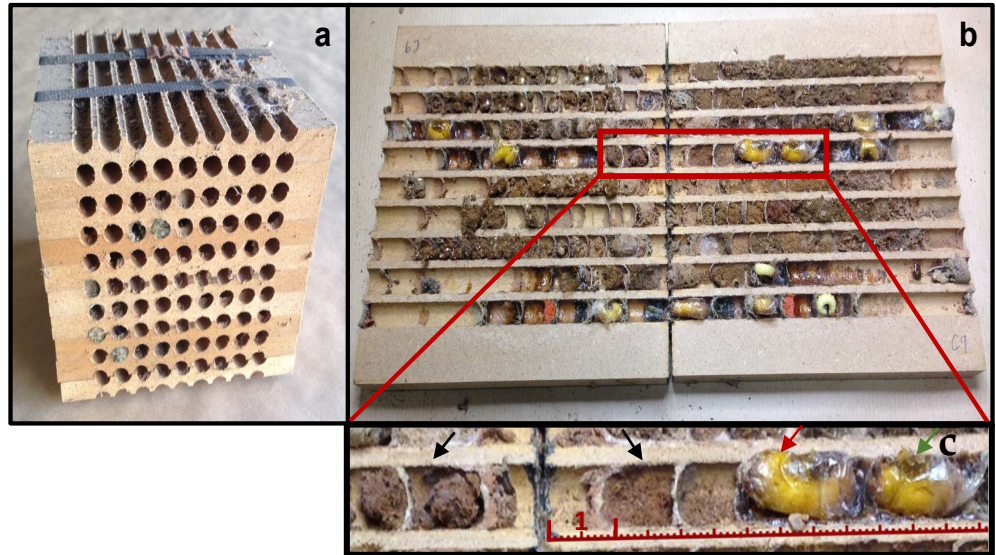
Figure 1.1 (**a**) Trap nests made of grooved boards stacked together in a solid block. (**b**) Opened individual grooved board showing the upper part (left) and lower part (right) of the same tunnels. (**c**) Detail of cohabitated tunnel with parasitized *Osmia* cocoons in the inner cells (black arrows), *M. sculpturalis* female prepupa situated next to *O. cornuta* cells (red arrow) and *M. sculpturalis* male prepupa (green arrow).

1.2.1 Study Area and Sampling

In January 2018, we placed four trap nests in two towns south of Turin (north-western Italy). The locations were chosen since the presence of *M. sculpturalis* had been reported nearby in previous years. The climate is typically continental, with cold winters and moderate summers (Bucci et al., 2017). The mean annual temperature is 12.5 °C, and the mean annual rainfall is 900 mm (Acquaotta et al., 2016).

We used two private gardens, one close to the hilly Monte San Giorgio natural park and the other encircled by farmland (municipalities of Piossasco and Volvera, respectively) (Figure S1).

Each trap nest consisted of a medium density fibreboard block of 20 × 20 × 15 cm made by a series of individual boards grooved with channels (also called

grooved boards or laminates), which were stacked together to form 81 tunnels of 1 cm diameter (Figure 1). To avoid the effect of the cavity size on the alien bee sex progeny (Bosch & Kemp, 2002; Seidelmann et al., 2016), all nesting cavities had the *M. sculpturalis* preferred diameter of 9.5–10 mm (Geslin et al., 2020; Quaranta et al., 2014), which overlapped with the accepted diameters for other solitary wild bees (Seidelmann et al., 2016). Trap nests were secured on walls between 2–4 m above the ground and sheltered from rain.

Trap nests were opened to analyze their content during late November 2018, when the wild bee nesting season ended. For each nest, we recorded the number of intact brood cells, the number of cells attacked by natural enemies, their position inside the tunnel and the species (if possible). The low diversity of species in trap nests allowed us to identify them during opening. The species' identity was confirmed after adult emergence. Natural enemies were identified using studies by . Fliszkiewicz et al., 2012; M. Krunić et al., 2005; Majka et al., 2007; Zajdel et al., 2014. We only kept and reared intact brood cells using specimens that had reached the prepupal or adult stage, depending on the species (Figure 1c). Prepupae and cocoons were then wintered separately in glass vials, in complete darkness, inside an environmental chamber at ambient temperature. During spring and summer 2019, we checked specimens every three days, and we identified the sex and weight at emergence. When adults did not emerge, we inferred the sex from the cell size and the sex of bees in the neighbouring cells, according to Seidelmann's methods for protandric solitary bee species (Seidelmann, 2006a).

1.2.2 Data Analysis

 Offspring Traits and Parasitism

We compared the progeny weight between sexes using a linear model after having log-transformed the weight to reach normality. The model did not improve when taking into account the nest as a random effect, so it was not included. Then, focusing on *M. sculpturalis* progeny, we calculated the observed sex ratio and the expected one according to Fisher's sex allocation theory. In particular, the theory

predicts that the parental investment must be divided equally between sexes in panmictic populations (Bosch & Vicens, 2005; Fisher, 1930a). In this context, for sexually dimorphic species, the progeny sex ratio is expected to be proportionally biased toward the sex with the lower investment.

The expected frequencies were calculated based on Torchio and Tepedino's formula (Torchio & Tepedino, 1980b), where the expected sex ratio is equal to the ratio between the mean female weight and mean male weight. The sex ratio and expected frequencies were calculated individually for each trap nest. The comparison of the observed sex ratio with the expected one was tested for each nest through a paired t-test. Furthermore, we aimed to compare these observed and expected sex ratios with the sex ratio recorded by open access global data. We used *M. sculpturalis* distribution data collected from two sources, either entomology collections or field observations, available in the Global Biodiversity Information Facility (GBIF) (*Global Biodiversity Information Facility. Free and Open Access to Biodiversity Data. GBIF Occurrence Download*, 2021). Records that did not include sex identification were removed. Then, data were grouped between observations in the native area (China, Korea and Japan) and those placed in the new colonized area (North America and Europe). Records without a location assignment but dated before 1993 were assigned to the native area since the species has never been reported outside its native range before this year (Hinojosa-Díaz, et al., 2005). The sex ratio was calculated separately to verify changes in the sex allocation strategy between the native and colonized areas. The proportions of females and males from the two areas were compared through a chi-square test. We assumed that the effect of bias in the sex detection, due to how the GBIF data were collected, was negligible.

The parasitism rate was computed as the ratio between parasite-infected cells divided by overall bees belonging to the same species.

All statistical analyses were carried out with the R software (version 3.5.1) using the lme4 package (Bates et al., 2011).

1.3 Results

1.3.1. Above-ground Nesting Community

The two species, *M. sculpturalis* and *O. cornuta*, occupied 229 out of a total of 324 available tunnels, and none of the trap nests were colonized by further wild bee species. Overall, 25% of nests were built by *M. sculpturalis*, while 75% were built by *O. cornuta* (Table 1). For both species, the nests consisted of a series of female brood cells (the later-emerging sex) in the inner part of the nest tunnel and a series of males (the earlier-emerging sex) at the entrance.

Table 1.1 Cavity-nesting bees and their natural enemies in trap nests.

Species	Nests (Occupied Tunnels)	Total Brood Cells	Mean Number of Cells per Nest	Maximum Number of Cells per Nest *	% of Parasitized Brood Cells	Emerged Adults	Natural Enemies
Osmia cornuta	171	1013	5.9	15	93	12	*Cacoxenus indagator* *Chaetodactylus osmiae* *Melittobia acasta* *Monodontomerus obscurus* *Ptinus sexpunctatus*
Megachile sculpturalis	58	244	4.9	7	7	213	*Cacoxenus indagator* *Monodontomerus obscurus* *Ptinus sexpunctatus*

* Number of cells within a tunnel belonging to one species only.

1.3.2. Interaction between the Exotic and the Native Bee

We recorded the coexistence of both species cohabitating in 26 tunnels. 44% of tunnels occupied by the exotic bee were built under cohabitation despite empty tunnels being available (Figure S2 and Database in supplementary materials).

We observed a maximum number of nine brood cells within the cohabited tunnels. Inner tunnel positions were mostly occupied by *O. cornuta*, while the outer positions (toward the entrance) were filled by *M. sculpturalis* (Figure 1.2).
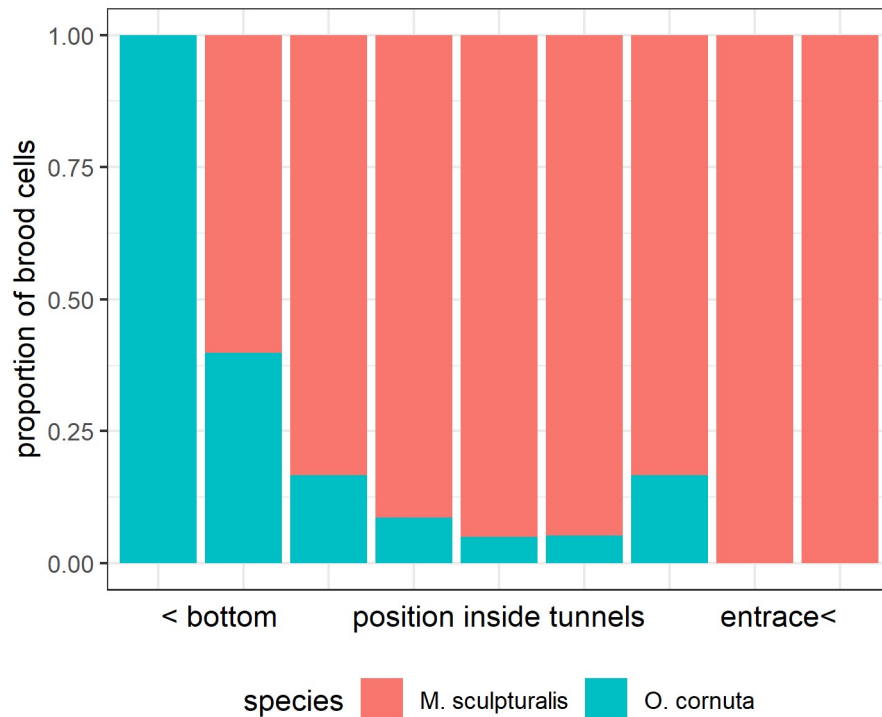
Figure 1.2. Proportion of species brood cells according to their position inside cohabitated tunnels, with a maximum of nine occupied positions (from the bottom to the entrance).

1.3.3. Progeny Weight and Sex Ratio of Exotic Bee

Female *M. sculpturalis* were significantly heavier than males ($\bar{x}$ male weight = 0.203 g, $\bar{x}$ female weight = 0.350 g, F = 129.1, df = 201, $p < 0.001$) (Figure 1.3a). We observed a sex ratio strongly biased toward males, resulting in 4.2 males for each female (Figure 1.3b). This result was significantly higher than the expected sex ratio estimated by the ratio between male and female weights (t = 3.48, df = 3, $p = 0.04$). Regarding the GBIF database, we found 331 records of *M. sculpturalis* from the native area and 351 from the new colonized area having a sex identification. The sex ratio was 1.72 and 0.91, respectively, in the colonized and native ranges. The former was very close to the predicted Fisher's sex ratio, while the latter was significantly lower than the sex ratio in the colonized range

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(χ^2 = 15.994, df = 1, $p < 0.001$) and, in turn, highly different from the observed sex ratio (Figure 1.3b).
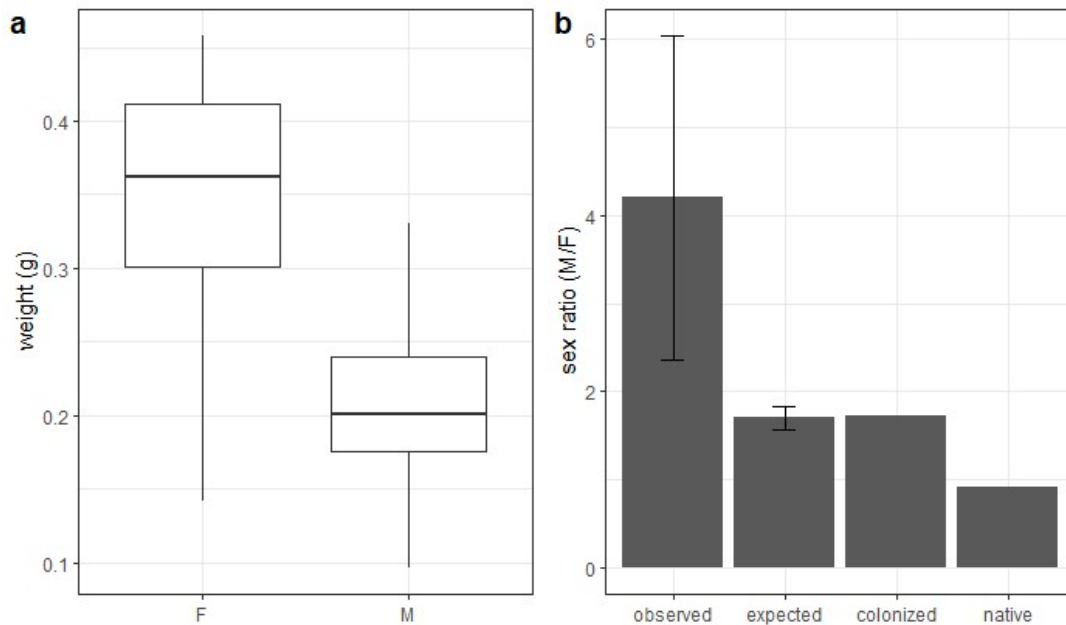
Figure 1.3. Progeny weight and sex ratio of *M. sculpturalis.* (**a**) Boxplot of female and male weights; (**b**) sex ratios (male/female) and standard error for observed nests, expected sex ratio according to Fischer's sex allocation theory (see Section 2.3.1. for details) and sex ratio calculated using GBIF data, respectively in the colonized and native areas.

1.3.4. Natural Enemies

Most *O. cornuta* cells were parasitized, and as a consequence only 12 bees emerged from stored cocoons. In contrast, 213 *M. sculpturalis* adults emerged from 244 brood cells. Five species of natural enemies were found infesting 93% of *O. cornuta* cells (Table 1). Among these natural enemies, three parasitized *M. sculpturalis* as well: *Cacoxenus indagator*, *Monodontomerus obscurus* and *Ptinus sexpunctatus* (Figure 4). However, these enemies were found exclusively in 7% of overall alien bee brood cells.

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Figure 1.4. Natural enemies found in *M. sculpturalis* brood cells. (**a**) Prepupae of *Monodontomerus obscurus (*right) next to intact *M. sculpturalis* prepupa (left). (**b**) Larvae of *Cacoxenus indagator* (right).

4. Discussion

The fast spreading of *M. sculpturalis* and its aggressive nesting behavior suggested a likely successful invasive performance (Lanner et al., 2020b; Le Féon et al., 2018; Polidori & Sánchez-Fernández, 2020). Novel empirical evidence on the interactions and traits of introduced species can indicate if they are thriving in the new location. Moreover, the understanding of how the alien wild bee impacts the native fauna is a challenging and complex issue (Russo, 2016); hence, investigations that highlight interaction mechanisms are useful for understanding what impacts should be expected. In this study, we found broods of *M. sculpturalis* and *O. cornuta* cohabitating inside the same tunnels. This evidence, together with the different phenologies of the two species, may implicate an interaction mechanism, which negatively affects the native bee. The fact that the exotic bee occupied outer positions (i.e., toward the entrance) in cohabitated tunnels is the result of its later nesting period, following that of *O. cornuta.* In addition, exotic brood cells are sealed with resin and remain locked until the following summer. Consequently, the spring-emerging *O. cornuta* from the inner

positions of the tunnel may get trapped, due to the barrier of resin and *M. sculpturalis* cell contents blocking the *Osmia* emergence. Previous studies have consistently demonstrated that *M. sculpturalis* is capable of evicting pre-adult stages of other bees from their cells (Lanner et al., 2020b; Laport & Minckley, 2012b; Le Féon & Geslin, 2018; Roulston & Malfi, 2002; Zandigiacomo & Grion, 2018). Thus, our results indicate the possibility of a potential combining effect of direct (eviction) and indirect competition (emergence blocking) acting at different times on the same nests. In this study, we detected the interaction with one native bee species only, probably because of a low richness of cavity-nesting bees in the study areas and the exclusive cavity diameter used in our trap nests. However, it is expected that other species of the genera *Osmia, Anthidium* and *Xylocopa* might be affected by the abovementioned mechanisms (Le Féon et al., 2018; Quaranta et al., 2004), although emergence blocking should only occur in earlier-emerging species, particularly in *Osmia* sp.

In the assessment of the progeny sex ratio, *M. sculpturalis* showed a greater male unbalance than expected, based on Fisher's theory of parental investment and sex allocation (Fisher, 1930b). This result is in agreement with the high proportion of males (83%) found by Geslin et al. in southern France (Geslin et al., 2020). A recent research on the genetic variability of the giant resin bee provides insights into the skewed male sex ratio, as it detected a high percentage of diploid males among individuals sampled in Vienna (Austria) (Lanner et al., 2021). Diploid males are probably the consequence of a founder effect in new colonized areas. Furthermore, it has been discovered that a low genetic diversity and the associated skewed sex ratio, even if temporarily limiting the performance of invasive species, do not always limit their spread over time, as theoretically expected (Darrouzet et al., 2015; Gloag et al., 2016). In particular, in invading social species, the haplo-diploid system is capable of overcoming the issue through multiple introductions (Lanner et al., 2021; Russo et al., 2021) and

natural selection mechanisms, which increases average heterozygosis at the sex locus over time (Gloag et al., 2016).

Despite the expectation of a higher male-biased sex ratio as a common pattern in a new colonized area, we found that the sex ratio of the *M. sculpturalis* from global data met the theoretical Fisher's prediction. Therefore, it seems that the overall exotic population did not suffer from a skewed male sex ratio like our local Italian population and the French one showed. This result also suggests that the unbalanced sex ratio might be a location-dependent limiting factor for the alien bee. Additionally, the sex ratio from native ranges were lower than expected. We believe that our results should be considered as baseline data to verify whether the skewed sex ratio is a factor involved in the *M. sculpturalis* invasion dynamic.

It has been argued that the success of a biological invasion might be facilitated by the invader species escaping from their natural enemies and by the modification of parasitism relationships in new locations (Dunn, 2009). While a parasite introduction due to the spread of an alien species may occur, invasive species can act as new hosts and also acquire parasites from native species (Jones & Brown, 2014). We detected three generalist natural enemies (Jones & Brown, 2014) in the exotic brood cells that were also present in *O. cornuta* cells. Two of them (*Cacoxenus indagator* and *Monodontomerus obscurus)* have a European native range (de Jong et al., 2014), while the third (*Ptinus sexpunctatus*) has a Paleartic distribution, and thus it should be present in the *M. sculpturalis* original range. Our observations provide the first record of parasitism in *M. sculpturalis* in the European territory. Despite potential adverse consequences of this parasite acquisition for the exotic bee, it was the most successful species in terms of emerging adults, and the overall parasitism rate was very low (7%) compared to that of *O. cornuta* cells (93%). This suggested that *M. sculpturalis* was potentially less susceptible to natural enemies than the native bee.

The novelties introduced in this study are essential knowledge on the competitive dynamic between native and alien bees, on species-fitness traits and on the incidence of natural enemies. Our results indicate that the giant resin bee might be a competitor with the native *O. cornuta* for nesting resources. Future studies using nesting traps and long-monitoring data will help to characterize the impacts of this fast-spreading exotic bee.

Appendix A

Table A1. Progeny weight differences and sex ratios in adult *M. sculpturalis*.

Nest	F	Mean Weight (g)	M	Mean Weight (g)	Observed Sex Ratio	Expected Sex Ratio
A	11	0.353	46	0.205	4.2	1.7
B	10	0.352	39	0.215	3.9	1.6
C	15	0.341	53	0.199	3.5	1.7
D	4	0.370	30	0.199	7.5	1.9
Total	40	0.350	168	0.203	4.2	1.7

Chapter 2. Insights on pollen specialization and maternal investment in two solitary bee species of genus *Osmia*

2.1 Introduction

Solitary bees of genus *Osmia* are a widely group of species that is known to be mostly polylectic. As generalist bees, they forage from multiple plant families for pollen provisions, although they can vary greatly in their local specialization when foraging for either a genus or a family of flowering plants. For example, it has been noted that *O. bicornis* may prefer trees as main floral sources (Coudrain et al., 2016). On the other hand, several studies have showed that *Osmia* populations are capable to adapt its foraging strategy in function of habitat and quality of main pollen sources (Radmacher & Strohm, 2010; Splitt et al., 2021). However, recurring patterns of bee choices are poorly understood in terms of individual females' choices. How a mother's provisioning patterns are related with maximization of reproduction success are little known. Moreover, these provision patterns could change throughout the season and influence reproductive parameters.

The provision stocked in a single cell by a female is the only food source for the developing larva, thus it determines the body size of the adult (Bosch and Vicens 2002, Seidelmann, 2006). Particularly in bees, maternal investment is adjusted by the mother to a very fine scale by stocking pollen and nectar gradually within brood cells. In a study based on the analysis of free flying females, Seidelmann et al. (2010) found that body size of mothers is a key condition to determine individual strategies in nesting females of solitary bees. Although the sex ratio in the population was balanced and met the Fisherian sex ratio, individual mothers allocated in the sexes according to their body mass.

Knowledge on bee diet preferences could reveal which plant species are important for their survival and reproduction and could be translated into important decisions concerning the planning and management of floral resources, for example, what species to plant to support wild bees populations (Casanelles-Abella et al., 2021).

Because quality of pollen provisions is a crucial resource for offspring development and energetically expensive for mothers to forage, maternal investment on pollen quality is probably tuned by mothers and influence developmental success of their progeny. In this experiment, through the analysis of pollen in larval diet I firstly, evaluated 1) if plant composition of provisions are different between females of *O. bicornis* and *O. tricornis* Latreille and 2) whether pollen diet of the offspring may influence the developmental stage reached. We hypothesized that diversity and quality of pollen provisioned is shaped by maternal investment choices like cell production, progeny sex ratio and provision mass to maximize fitness.

2.2 Materials and Methods

2.2.1 Study organism

O. bicornis and *O. tricornis* are univoltine, polylectic and protandrous species (males emerged earlier than females from cocoons) (Sedivy & Dorn, 2014). Both species nest in pre-established cavities and their nest consists of a series of cells provisioned with a mixture of pollen and nectar to nourish their larvae. The cells contain one egg each and are separated by mud partitions. *O. bicornis* and *O. tricornis* both are mid and late spring flying masons bees (April to June) (Splitt et al., 2022; Vicens et al., 1994) .

Both species start emergence in April, coinciding with the decline of the nesting activity of *O.cornuta* (Splitt et al., 2022; Vicens et al., 1994). Males emerge first,

followed three to seven days later, by females. Upon emergence, males fly in zig-zag in front of their nest and then fly away to take nectar (they were seen on apple and *Borago officinalis* flowers). After returning to the nesting area, they await female emergence. Mating takes place as soon as females emerge, normally in the vicinity of the nests.

O. bicornis and *O. tricornis* collect pollen from a very broad spectrum of plants, while *O. cornuta* prefers Rosaceae, especially fruit trees. Both species are especially important in fruit tree pollination in orchards due to their specific foraging and nesting behavior (Vicens et al., 1994)

As most of the megachilid bees, they show a sexual dimorphism in body size with females being around 1.6 times heavier than males (Seidelmann et al., 2010).

2.2.2 Study area and sampling

The study was conducted in the Campus Bellaterra, Autonomous University of Barcelona, Spain. The area is in a heterogeneous patchwork of from urban fragments (40%) and agriculture lands and forest (60%) that range from pine forests to holm oaks forest.

During May and June 2021, we analyzed nests from free flying females of two species of red mason bee (*O. bicornis* and *O. tricornis*) at two artificial nesting shelters. Red mason bees were released from loose cocoons wintered at 4 °C since October 2020. The two nesting shelters we set up with wooden boxes held at 1.5 m above the ground. They consisted of 8 and 10, respectively, wooden nest blocks containing 250 nesting holes each, filled with paper straws (7 mm diameter × 150 mm length).

To quantify maternal investment of individual marked females, we checked daily their nesting activity throughout their cell production lifetime. We released males in the two nesting shelters 5-10 day before female releasing. Two or three days after female releasing, we tagged in the field only flying females that were seen starting a nest (provisioning holes with pollen, nectar, or mud). Each nest was

assigned to a marked female. Paper straws were pulled out to record date of start, the daily progression, and the date of the closure of nests. By this method we were able to record nearly the whole cell production lifetime of 47 individual females which constructed 538 brood cells in the shelters. Because competition for nesting holes and usurpation among mothers is common, in the case of nest usurpation, we split up the nest based on the daily cell progression, and the cells were associated to the respective bee.

During the autumn and the winter, the occupied nests by marked bees were open and analyzed. The content, weigh, position, length and sex of every cocoon were recorded. The weight of every cocoon with an adult bee inside was determined with a laboratory balance to the nearest 0.1 mg. To calculate the cocoon mass of parasitized or killed progeny (those who had not reached adulthood inside cocoons) the cocoon weight was estimated from the mean cocoon masses of the appropriate sex of the same bee offspring. Bees were sexed through the clypeus hair color after opening the cocoon with a sharp pair of scissors. If the content of a cell was parasitized or not developed as a cocoon, the sex of the killed larvae was inferred from the cell position, cell length and the sex of the bees in the neighboring cells (Holm, 1974; Maddoks & Paulus, 1987; Raw, 1972; Seidelmann, 2006b). The parasitism rate was determined as the number of cells parasitized per total number of provisioned cells in the nest (Seidelmann, 2006b).

We estimated expected sex ratio by the mean weight of male cocoons compared with the mean weight of female cocoons. This difference in the body weight is considered a proxy of the expected sex ratio based on Torchio and Tepedino's formula (Torchio & Tepedino, 1980b).

2.2.3 Pollen sampling and analysis

To know whether different developmental stages are determined by nutrition on different plants we analysed pollen composition of post-emergence residues (pollen contains in the faeces) following a similar protocol used by Tobajas et al. (Tobajas et al., 2022). To evaluate individual differences of mothers providing

pollen and nectar related with the successful development of their offspring, we selected two brood cells per each one of 12 tagged nesting females ("mothers") which produced brood cells that reached one of the two developmental stages: pre-wintering prepupae or pre-wintering adult. Fecal masses of a total of 24 brood cells belonging to these "mothers" were sampled and divided in two categories according to the developmental stage: 12 prepupae and 12 adults (for practical purposes, I will refer henceforth as "pupae").

To analyse pollen we applied the morphological identification method using the frass residues (the pollen contained in the faeces) which provide full details of the pollen contents in every brood cell (Ferreira & Absy, 2013). For some of the samples it was not necessary to expose de pollen grains to an acidic medium because of the digestive process. For almost half of the samples it was used the most widely adopted chemical process, the acetolysis (Erdtman, 1960) which exposes pollen grains to an acidic medium that destroys its content, allowing assessment of the morphological characteristics of the walls of pollen grains and, consequently, their identification.

At least 300 pollen grains from each sample were counted, and lines were established across the cover slip at 400x magnification. The pollen grains were identified to the genus level because of the difficulties associated with a finer taxonomic assessment. A pollen atlas and an dichotomous keys were employed (Moore et al., 1991; Reille, 1998) for the identification. In most cases, it was possible to reach the "pollen type" level only, which consider a common morphology for several genera or species (e.g., "*Aster* type" includes some genera from Asteraceae family). Pollen richness (number of different pollen types in the brood cell) and pollen diversity (Shannon diversity index (H')) were calculated for each sample.

2.2.4 Data Analysis

To identify the main pollen resources in the diet of *O. bicornis* and *O.tricornis* offspring, we calculated the percentage of each pollen type from the total sample

processed. To determine whether pollen richness and pollen diversity had significant effects on the developmental stage reached (pupa or adult), we used nonparametric statistics. The Mann-Whitney test was used to compare richness (number of different pollen types in the brood cell) and pollen diversity (Shannon diversity index (H')) of pollen genus/types in samples between two categories: bee species, stage of development and season, periods. The Spearman correlation test was used to look for linear correlations between sets of data. The Kruskal-Wallis test was used to compare medians between two or more samples, respectively.

2.3 Results

2.3.1 Population parameters

A total of about 70 females were tagged provisioning 538 brood cells in the two shelters. Of them, only 47 nesting females were used for analysis because they were observed provisioning regularly and were reliably assigned to their nests. From the majority of the 538 brood cells studied (133 females and 405 males), we obtained the bee imagoes, but 111 individuals did not reach the adult stage, interrupting the development in the prepupal stage.

Table 2.1. Nests and cells produced by females of the two species in shelters.

Trait	*O. bicornis*	*O. tricornis*
Total number of brood cells	223	315
No. of mothers	21	28
Sex ratio (m/f)	6.05±1.99	3.25±1.6
Cell number per nest	4.3	4.7
Parasitism rate	0.36	2.1
Body weight sons (mg)	63.5±13.5	66.7±8.2
Body weight daughters (mg)	114.7±22.9	117.1±9.7

2.3.2 Pollen analysis

A total of 14 different pollen types were found in the 24 brood cells analysed. The most abundant families in the brood cells were Fagaceae (*Quercus* spp) e Rosaceae (Fig. 2.1) for *O. bicornis* and *O. tricornis* respectively. The other pollen types were more infrequent.

Table 2.3 Pollen type percentages in the brood cells of the two different species

Pollen type	*O. bicornis*	*O. tricornis*
Quercus	7.5	0.1
Quercus ilex morphotype	53.4	16.9
Pinus	<0.1	<0.1
Rosa	9.7	9.3
Rubus morphotype	11.7	21.5
Rosaceae cf. Spiraea	17.1	48.9
Anthemis morphotype	0	<0.1
Aster morphotype	0	<0.1
Brassica morphotype	<0.1	0
Echium	0.3	3.2
Papaver rhoeas morphotype	0.1	<0.1
Poaceae	<0.1	<0.1
Ridolfia morphotype	0	<0.1
Ranunculus morphotype	0.1	<0.1
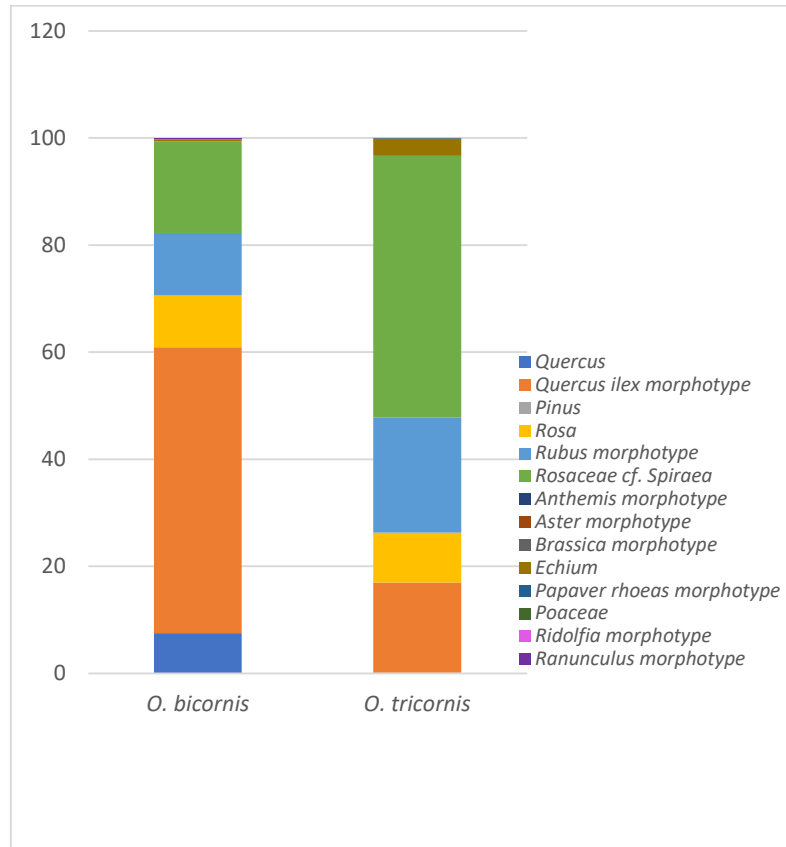
Figure 2.1 Pollen type proportion in the brood cells of the two different species.

The average pollen richness in the brood cells was 4.8 and the average pollen diversity was 0.83. We have not found significant differences on pollen richness and pollen diversity between pupae and adults for any of the mason bee species (Mann-Whitney test: U = 246, n1 = 12, n2 = 12, P = .12).

Pollen proportions between diets of pupae and adults were not significantly different. However, individuals who did not reach the adult stage feed more on the pollen types that were not predominant in the species pollen mixture (Fig. 2.2).
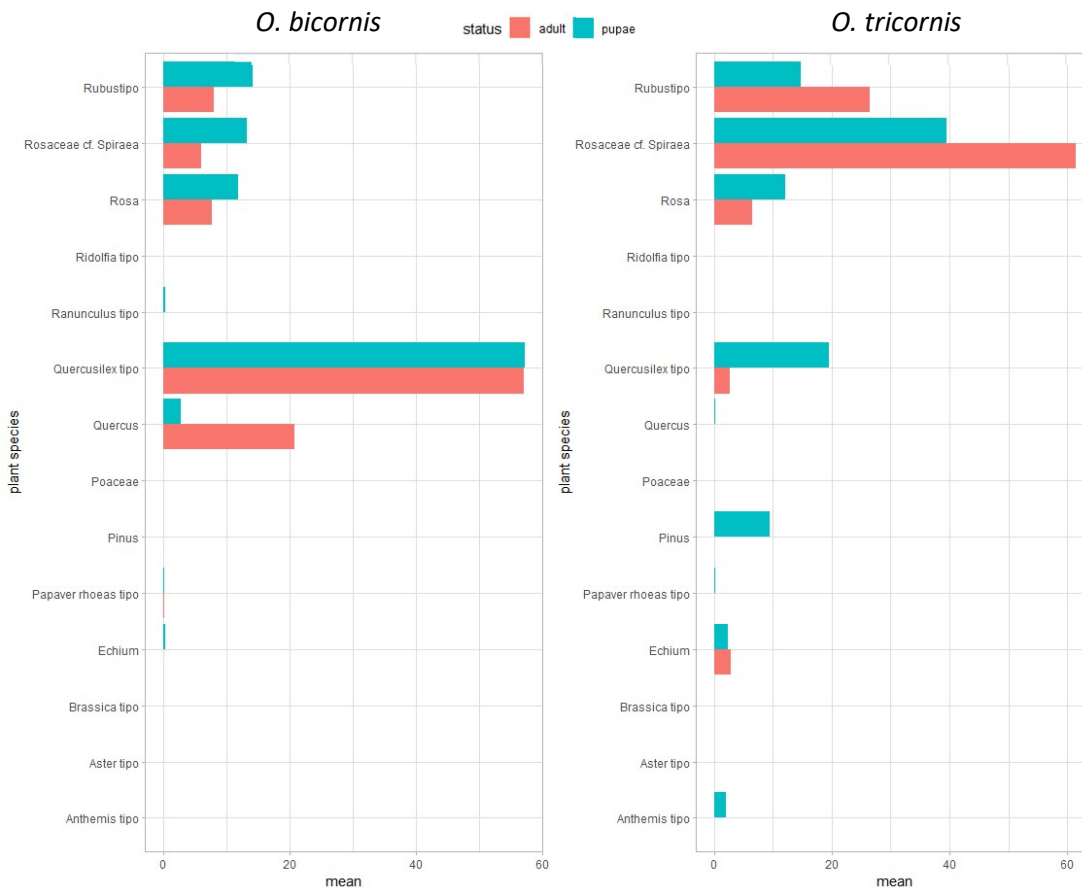
Figure 2.2 Pollen type proportion divided by the different classes of offspring among species: brood cells with adults (red) and brood cells with pupae (blue).

Pollen types belonging to Fagaceae are prevalent in the brood cells made in May and early June. Instead, Rosaceae pollen type is the most common in June (Fig. 2.3 and 2.4).

The pollen types of woody plants were predominant in all the samples (> 90%). Among the herbaceous plants, only the pollen of *Echium* (L.) reached significant percentages (2.6% as average; and 9,6% as maximum).

Figure 2.3 Summary of the pollen type used by each brood cell of *O. bicornis* along the season and grouped by their tagged female.
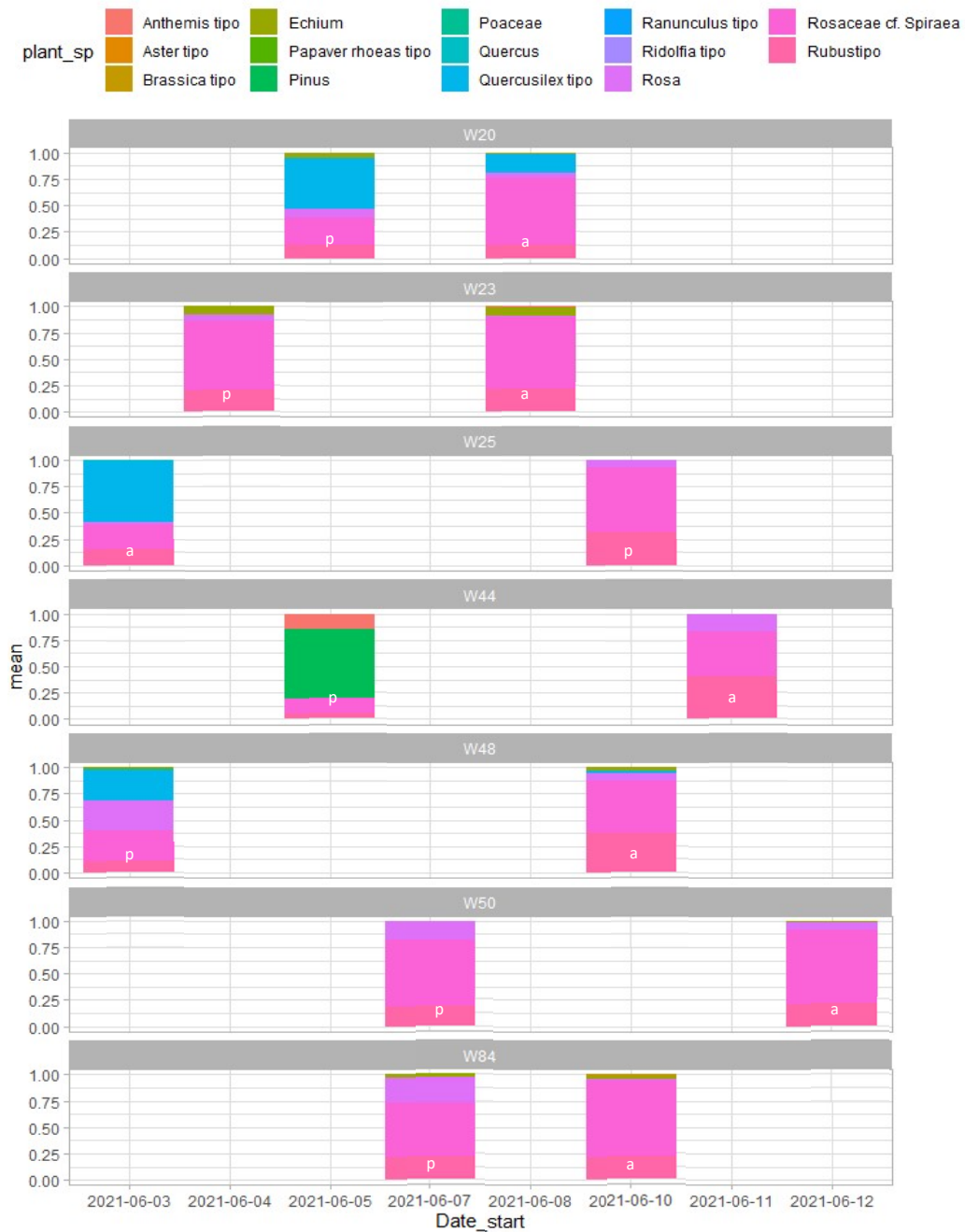
Figure 2.4 Summary of the pollen type used by each brood cell of *O. tricornis* along the season and grouped by their tagged female.

2.4 Discussion

Examination of pollen from nests of *O. bicornis* and *O. tricornis* showed that even when the two similar species nested simultaneously and at the same locality, more than 50% of the pollen they collected was from different plant families.

Over 70% of the pollen collected by *O. bicornis* was from *Quercus* which produce little or no nectar and the bees obtained nectar from different species that probably represented the lower percentages in the pollen mixture. In nests of the two species, pollen of a single taxon averaged 60% or more. These polylectic species are capable of exploiting a variety of resources from the plant families present in the area, but exhibiting a pronounced affinity for the pollen of *Quercus* and Rosacea, respectively, in the case of *O. bicornis* and *O. tricornis*.

The present study shows that adult development of the two species is not affected by a particular pollen mixture in larval diet. Correspondingly, the results suggested that neither the developmental stage of the offspring nor the final adult weight are affected by the different pollen mixture they eat. This result is in agreement with the lack of effects of pollen richness and pollen diversity found by Tobajas et al. (2022) in *Osmia caerulescens* (Linnaeus). In this study the pollen composition did not differ among brood cells harbouring adults, larvae, and pupae.

These findings strongly suggest that the larvae of both species can benefit from a diet composed over 60% from one taxon of plants and is being negatively affected by the change of season in which the predominant pollen type started to be rare.

On the other hand, we observed that the proportion of rare pollen (plant species with < 5% of pollen diet) was higher in the failed individuals (those pupae that

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did not give rise to adults). Some of these pollen types are particularly rich in protein but contains toxic components, such as pyrrolizidine alkaloids in high concentrations in the case of *Echium* (Bopprè et al., 2008), which might be the cause of unsuccessful development in generalist bees (Sedivy et al., 2011).

The analysis of pollen extracted from post-emergence residues has been revealed as a useful method to determine pollen collection and consumption, providing accurate information about the use of trophic resources.

Chapter 3. The role of gardens in the conservation of insect pollinators: The case of pollinator-flower interactions in gardens during the COVID-19 pandemic lockdown of 2020

Ollerton, Jeff*, Trunschke, Judith, Havens, Kayri, Landaverde-González, Patricia, Keller, Alexander, Gilpin, Amy-Marie, Rodrigo Rech, André, Baronio, Gudryan J., Phillips, Benjamin J., Mackin, Chris, Stanley, Dara A., Treanore, Erin, Baker, Ellen, Rotheray, Ellen L., Erickson, Emily, Fornoff, Felix, Brearley, Francis Q., Ballantyne, Gavin, Iossa, Graziella, Stone, Graham N., Bartomeus, Ignasi, Stockan, Jenni A., Leguizamón, Johana, Prendergast, Kit, Rowley, Lisa, Giovanetti, Manuela, De Oliveira Bueno, Raquel, Wesselingh, Renate A., Mallinger, Rachel, Edmondson, Sally, Howard, Scarlett R., Leonhardt, Sara D., Rojas-Nossa, Sandra V., Brett, Maisie, Joaqui, Tatiana, Antoniazzi, Reuber, Burton, Victoria J., Feng, Hui-Hui, Tian, Zhi-Xi, Xu, Qi, Zhang, Chuan, Shi, Chang-Li, Huang, Shuang-Quan, Cole, Lorna J., Bendifallah, Leila, Ellis, Emilie E., Hegland, Stein Joar, Straffon Díaz, Sara, Lander, Tonya Allen, Mayr, Antonia V., Dawson, Richard, Eeraerts, Maxime, Armbruster, W. Scott, Walton, Becky, Adjlane, Noureddine, Falk, Steven, Mata, Luis, Goncalves Geiger, Anya, Carvell, Claire, Wallace, Claire, Ratto, Fabrizia, Barberis, Marta, Kahane, Fay, Connop, Stuart, Stip, Anthonie, Sigrist, Maria Rosangela, Vereecken, Nicolas J., Klein, Alexandra-Maria, Baldock, Katherine and Arnold, Sarah E. J.

*Corresponding author

Author affiliations are included at the end of the article

Abstract

During the main COVID-19 global pandemic lockdown period of 2020 an impromptu set of pollination ecologists came together via social media and personal contacts to carry out standardised surveys of the flower visits and plants in gardens. The surveys involved 67 rural, suburban and urban gardens, of various sizes, ranging from 61.18° North in Norway to 37.96° South in Australia, resulting in a data set of 25,174 rows, with each row being a unique interaction record for that date/site/plant species, and comprising almost 47,000 visits to flowers, as well as records of flowers that were not visited by pollinators, for over 1,000 species and varieties belonging to more than 460 genera and 96 plant

families. The more than 650 species of flower visitors belong to 12 orders of invertebrates and four of vertebrates. In this first publication from the project, we present a brief description of the data and make it freely available for any researchers to use in the future, the only restriction being that they cite this paper in the first instance. The data generated from these global surveys will provide scientific evidence to help us understand the role that private gardens (in urban, rural and suburban areas) can play in conserving insect pollinators and identify management actions to enhance their potential.

Keywords: bees, flowers, hummingbirds, insects, pollination, species interactions

3.1 Introduction

Pollinators such as flies, bees, moths, birds, and bats are important components of ecosystems and provide crucial functions and services by facilitating the reproduction of most wild plant species and crop varieties (A.-M. Klein et al., 2007; Ollerton et al., 2011; Rodger et al., 2021). However, the diversity and abundance of pollinators have declined in some parts of the world, largely driven by land use changes and agricultural intensification, with concomitant effects on seed set (Millard et al., 2021; Ollerton, 2017; Ollerton et al., 2011; Potts et al., 2010). Domestic and public gardens are increasingly recognised as potential synanthropic hotspots of pollinator diversity within the matrix of human-dominated landscapes that characterises many parts of the world, and as areas that deliver multiple ecosystem services, including pollination of fruit and vegetable crops (Baldock, 2020; Bendifallah & Ortiz-Sánchez, 2018; Camps-Calvet et al., 2016; Davies et al., 2009; Erenler, 2013; Fitch et al., 2019; Foster et al., 2017; Levé et al., 2019; Majewska & Altizer, 2020; Marín et al., 2020; Matteson et al., 2008; Norfolk et al., 2013, 2014; Prendergast, 2022; Prendergast & Ollerton, 2021; Tew et al., 2021). However, the effectiveness of gardens in

supporting pollinators varies according to taxon, locality, garden management, and generalization specialization range of occurring interactions, especially in urban areas (Baldock, 2020; Maruyama et al., 2019; Prendergast et al., 2022; Tew et al., 2022; Theodorou et al., 2020). To date, surveys of pollinators and their interactions with garden plants have usually been constrained in their geographical scope. This limits our understanding of the diversity of pollinators associated with gardens and how they vary globally, and our ability to answer questions such as: Do pollinators interact similarly with flowers in different parts of the world? How are different types of garden crop plants integrated within the wider network of plant-pollinator interactions? Does the role of super-generalist species such as honey bees (*Apis* spp.) vary according to region and garden type? What is the relative value of native versus non-native plant species to pollinators and how does this vary geographically? There is thus a clear need for more geographically extensive data on the relationships between pollinators and garden plants to have a better understanding of how this varies globally and to identify plant species in different regions that are important for supporting pollinators, particularly early and late in the season when little else may be in flower other than exotic garden plants. It could also help us to understand the pollinator and plant traits that distinguish garden communities from non-garden communities. Increasing our understanding of garden pollinators will help identify actions that gardeners can take to support these declining insects. During the lockdown precipitated by the COVID-19 pandemic of 2020, which limited the movement of individuals within and between countries, the lead author coordinated an ad hoc network of ecologists to collect standardised data on plant-pollinator interactions from gardens to which they had access. The purpose of this impromptu project was fivefold: (1) To take advantage of a difficult situation that would allow ecologists to focus more time and effort into understanding the ecology of their own gardens; (2) To generate a standardised data set that could be used by researchers whose field work had been curtailed by the pandemic; (3) To help to improve the physical and mental wellbeing of those field based

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scientists whose access to nature was severely limited; (4) To build a data set that could be used to address unanswered scientific questions such as how the diversity of pollinators varies with garden size and geographic position, and how ornamental and food plants are used by the pollinators in home gardens; (5) To make the data freely available to give it significant future value beyond the immediate generation of research outputs, e.g. for teaching, informing extension and outreach efforts such as "best plants for pollinators", and so forth. In this initial paper from the project, we provide an overview of the data set and discuss how it may be used in the future, with encouragement for others to do so.

3.2 Methods

While recruitment of participants was on an ad hoc basis, all had previous experience of pollinator surveys and insect and plant identification in their region. Three protocols for garden data collection were used which we refer to as Type A, B and C surveys. Individuals chose to undertake one, two, or all three types depending on their personal circumstances and time availability. Type A surveys involved regular walks at a steady pace around the garden, recording the insects and other flower visitors that were active on particular flowers (representing potential pollinators, hereafter for brevity referred to as "pollinators"). Each walk was timed and the amount of time spent surveying was proportional to the size of the garden and the number of plants in flower present. For example, in the first author's 10 m x 20 m garden he undertook 15-minute walked surveys, always following the same route one way, then returning, pausing to record data. In addition, where possible, the number of inflorescences and flowering area of all plants in bloom were estimated regularly (area in m^2 and number of floral units), including both those plants that were visited and those not visited by potential pollinators. The frequency with which this occurred varied by observer but was typically whenever a change for a particular species seemed to be happening, most often weekly, or every 1-2 days during periods of rapid change if monitoring

was that regular. "Floral units" varied according to taxa, from individual flowers in the case of species with large, distinct blossoms (e.g., species of Malvaceae), to dense inflorescences in the case of many smaller Lamiaceae, or inflorescences (flower heads) functioning as single blooms in species of Asteraceae.

Type B surveys were based on the protocol for the UK Pollinator Monitoring Scheme (PoMS – see: https://ukpoms.org.uk/ and Carvell et al. 2016). This involved 10-minute timed observations focused on a patch of flowers belonging to one species, in an area no larger than 0.5 m x 0.5 m. The species were facultatively chosen by any observer according to their presence in gardens. The observer recorded all flower visiting insects as well as the number of flowers each pollinator visited and the number of flowers of the target species within the 0.5 m x 0.5 m area. Type C surveys were ad hoc observations of flower visitors made outside the formal periods in which Type A and Type B surveys were undertaken. We include these data as they comprise some rare interactions that were not observed during the formal survey periods, as well as observations by individuals who were not able to complete the Type A and B protocols. Surveyors were asked to prioritise the collection of data via Type A surveys and this constitutes the majority of the data (86.9%), followed by Type B (11.8%) and Type C (1.3%). In all cases, flower visitors and plants were identified to the lowest taxonomic level possible given the observer's skill and ability, most frequently species or genus. Identification advice was provided by local experts where required, using photographs or captured specimens. There were only 17 cases where the plant could not be identified beyond family, and 3,169 where identification was only to genus. These represented just under 13% of the records in the data set. For the flower visitors, almost 70% were identified to species level and only just under 18% could not be identified to at least genus. Two of the authors (JO and JT) have corrected spellings of species names and updated the taxonomy as far as possible, using a wide range of sources for the animals and the International Plant Names Index (IPNI) (www.ipni.org) for the plants. But anyone using the data in the future is advised to check it for accuracy.

3.3 The Data Set

Formal surveys took place between 16th March (day 76) and 14th October (day 288) 2020, though we also included some earlier ad hoc data that had been collected by participants. Data was collected by scientists from 14 countries, in gardens ranging from 61.18° North in Kaupanger, Norway to 37.96° South in Black Rock, Australia (Fig. 1). Metadata for each garden are provided and explained in Table 1 and an explanation of the elements within the data set is given in Table 2. The resulting data set comprises surveys from a total of 67 gardens, ranging in size from 5 m^2 to 8,000 m^2 in extent, and from 2 m.a.s.l to 2,655 m.a.s.l in elevation. Twenty-two of the gardens were in a rural setting, 14 in a suburban locality, and 31 were considered urban. Total observations in the gardens involved over 1,000 species and varieties of plants belonging to more than 460 genera in 96 flowering plant families. Importantly, this includes plants to which visits were not observed during the surveys, which provides important information about the relative importance of plants in different contexts. Almost 47,000 visits to the flowers of these plants were recorded, by more than 650 species of pollinators, belonging to more than 250 genera in 110 families. In total, the data set comprises 25,174 rows of data arranged in columns according to the headings shown in Table 1. In the data set, 1 row = 1 unique interaction record for that date/site/plant species, recording the flower visitor species and number of individuals or visits, or a zero-visit observation. The most frequently represented plant species that was visited by pollinators in these gardens was *Taraxacum officinale* (550 records of interactions, that represented 2.5% of the plants observed). The most frequent plant family visited was Asteraceae (2,540 records, 11.6% of the plants) followed by Brassicaceae (1,663 records, 7.6% of the plants) and Boraginaceae (1,214 records, 5.6% of the plants). The pollinator-dependent crop plants within the data set include plums (*Prunus domestica*), apples (*Malus domestica*), soft fruit in the genus *Rubus*, Brazilian pepper (*Schinus terebinthifolia*), coriander (*Coriandrum sativum*) and edible

Brassicaceae, mainly *Raphanus* and *Brassica* spp. The phylogenetic diversity of the pollinators extended across 12 orders of invertebrates, 10 of them insects, and four orders of vertebrates. The most frequently encountered pollinators belonged to the genus *Bombus* (2,566 records, 19.5% of the pollinators) whilst the single most common species was, unsurprisingly, the ubiquitous Western honeybee (*Apis mellifera*) with a total of 1,536 records (11.7%). Although we have not categorised the plants and flower visitors as native or exotic in the region in which the gardens were surveyed, this could easily be done and would provide important insights into the role of non-native flora in supporting pollinator populations, and the potential for species such as *A. mellifera* to compete with other pollinators.

Figure 1: Locations of the gardens surveyed in this study, globally (main map) and within Europe and the Mediterranean (inset 220 map).

Table 1: Explanation of the metadata for dataset. Note that where metadata are missing "NA" has been added.

Metadata item	Format	Description
Five letter identifier	Text	A code that identifies each garden
Surveyor(s)	Text	The name(s) of the individual(s) who carried out the surveys
Email address	Text	The latest email address of the lead individual surveyor
Locality	Text	The town, city or region where the survey took place
Country	Text	The country in which the survey took place
Latitude	Numerical	The decimalised latitude of the garden in which the survey was conducted. Accuracy is limited to two decimal places for reasons of privacy and security
Longitude	Numerical	The decimalised longitude of the garden in which the survey was conducted. Accuracy is limited to two decimal places for reasons of privacy and security
Elevation (m.a.s.l)	Numerical	The approximate elevation of the garden in which the survey was conducted in metres above sea level
Garden size (m²)	Numerical	The approximate size of the garden in which the survey was conducted in square metres
Type	Text	The locality of the garden in relation to its surroundings. Options are "urban", "suburban", "rural"
Trees?	Text	The presence or absence of trees in the garden. Options are "yes" or "no"
Shrubs?	Text	The presence or absence of shrubs in the garden. Options are "yes" or "no"
Lawn?	Text	The presence or absence of a lawn in the garden. Options are "yes" or "no"
Herbaceous perennials?	Text	The presence or absence of herbaceous perennials in the garden. Options are "yes" or "no"
Compost heap(s)	Text	The presence or absence of one or more compost heaps in the garden. Options are "yes" or "no"
Age of property (years)	Numerical	The approximate age of the garden
Other relevant information	Text	Some participants included additional information about their gardens

Table 2: Explanation of the dataset. Note that for some items, where data are missing "NA" has been added.

Data item	Format	Description
Five letter identifier	Text	A code that identifies each garden (refer to Metadata)
Survey type	Text	Refer to text. Options are "A", "B", "C"
Date	Text	The date in 2020 on which the survey was carried out. Format is DD/MM/ (day/month/)
Day of the year	Numerical	The day of the year on which the survey was conducted, with 1st January = 1
Start time	Numerical	The time at which the survey commenced, format = 24-hour clock
Duration (min)	Numerical	The length of the survey in minutes
Plant family	Text	The taxonomic family to which the observed plant species belongs
Plant genus	Text	The taxonomic genus to which the observed plant species belongs
Plant species	Text	The taxonomic identity of the plant species observed
Plant species comments	Text	Relevant information about the plant species concerned, e.g. the variety or common name
Total floral cover (m²)	Numerical/Text	The approximate area of flowers of that species. Values are numerical and in square metres, except for very small areas in which the "<" symbol has been used to qualify the number
Number of floral units	Numerical/Text	The approximate number of flowers or inflorescences present. In some cases, this has been qualified with a "+" symbol
Flower visitor order	Text	The taxonomic order to which the observed flower visitor species belongs
Flower visitor family	Text	The taxonomic family to which the observed flower visitor species belongs
Flower visitor genus	Text	The taxonomic genus to which the observed flower visitor species belongs
Flower visitor species	Text/Numerical	The taxonomic identify of the flower visitor species observed. A zero ("0") indicates that no flower visitor was observed
Sex/caste	Text	The sex ("male", "female") or bee caste "worker", "queen") when noted
Flower visitor species comments	Text	Some participants included additional information about the flower visitor species
Number of individuals	Numerical	The number of individual flower visitors observed
Number of flowers visited	Numerical	The number of floral units on which the flower visitor foraged
Photo or specimen taken?	Text	Whether or not a physical record of the flower visitor was preserved

3.4 Discussion

This is the largest data set of garden flower visitors ever assembled and is clearly a product of the COVID-19 pandemic; as such we hope that the circumstances under which the data were collected are never repeated. The pandemic, however, provided a unique opportunity for pollinator experts from across the globe to collaborate in the collection of valuable research data. One of the positive aspects of this has been that constraints on field work have resulted in a more local focus on biodiversity that has turned up some surprising results. For example, there is at least one case in our data set of confirmation of a bee species new to a country: *Megachile nigriventris* (Schenk), new to Belgium, discovered by Nicolas Vereecken. Similarly, the scarce UK species *Andrena labiata* (Fabricius) was discovered in the first author's garden, its only record in Northamptonshire in decades. Finally, a close focus on her garden in 2020 enabled Ellen Rotheray to describe the puparium and development site of the hoverfly *Rhingia rostrata* (Linnaeus), for the first time (Rotheray & Rotheray, 2021). This highlights the fact that even trained ecologists are sometimes not fully aware of the species present in their immediate vicinity. This paper is the first output from the data set and more will appear in the coming years as members of the team focus on a range of questions. For example: how does garden location and structure affect the patterns that we observe; are there differences between urban versus rural gardens; what influence does garden area and landscape structure (habitat area and connectivity) have on pollinator diversity; which ornamental plant species support pollinators of food plants? Our data should also contribute to discussions

about the value of native versus exotic garden plants for pollinators (Corbet et al., 2001; Garbuzov & Ratnieks, 2014; Giovanetti et al., 2020; Mata et al., 2021; Pardee & Philpott, 2014; Rollings & Goulson, 2019; Salisbury et al., 2015; Staab et al., 2020). With additional data gleaned from the literature it should also be possible to address questions such as: Do pollinators prefer plants of similar nutritional quality across the globe? Does the trait matching between flower and pollinators change in different gardens or continents? There are a number of potential biases within this data set that that must be acknowledged. The first is that the gardens of pollination ecologists may not be representative of those of the wider population. However significant garden heterogeneity has been documented in other studies of garden pollinators and resources (e.g. Prendergast & Ollerton, 2021; Tew et al., 2022). There were also a number of surveyors who were isolating with parents or other relatives and therefore not conducting surveys in their own gardens. In addition, a small number of the gardens were actually public spaces. We note also that during the lockdown period there was greater garden use by occupants, plus a decrease in road and air traffic, and other human activities, that might have influenced the patterns of flower visitation observed. There are further geographical biases with respect to where the participants lived. The project began as a UK-based initiative, though soon expanded as word spread, and hence there is a high proportion of data from the UK. As with most ecological studies, there is a lack of data from low-income countries, especially in the Global South, but if opportunities arise for additional surveys these could be added, and we would update the data set in Zenodo. Having said that, it's important to emphasise that the locations of the surveys do cover a wide range of climates and elevations, adjacent to a variety of biomes, in different levels of urbanisation, which makes this standardised data set a unique and valuable contribution to researchers interested in flower visitors and their nectar and pollen sources. In addition to these geographic biases, there will also be a non-random set of plants (and potentially pollinators) included within the surveys because gardeners usually choose plants for their perceived attractiveness

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and their climatic and edaphic tolerance of where they are planted. These in turn attract flower visitors that are able to exploit those flowers, and which may have a strong association with human settlements. However, rather than being biases per se, we would see these as interesting patterns that could be explored within the data set, for example looking at similarities in the plants and pollinators that widely different types of gardens host. Such phylogenetic patterns are not, of course, independent from geographical biases, nor are they separate from the issue of representativeness. As pollination ecologists, the participants are likely to be more aware than most of the importance of allowing "weeds" to grow that are important for pollinators, such as ragworts, dandelions, and clovers. But again, we see the future potential of comparing such gardens, in which herbicides and pesticides are infrequently or never used, with more typical gardens. The question of the representativeness, or otherwise, of our results is something that could be addressed in the future by comparing these data with previously published studies or by repeat-surveys of some of these sites. Although we have set up working groups to consider these questions, and others, we wish to make the data set freely available to anyone who wishes to use it in their research, especially those ecologists whose data collection opportunities were curtailed by the pandemic. We ask only that this paper is cited in return. Finally, we dedicate our paper, with our grateful thanks, to all of the front-line workers, health professionals and scientists who worked hard to steer the world through one of the most difficult periods in modern times.

APPENDICES Additional supporting information may be found in the online version of this article: Table S1. Site visited, their location and the number of times they were visited.

AUTHOR AFFILIATIONS

1   Faculty of Arts, Science and Technology, University of Northampton, Waterside Campus, UK

2   Kunming Institute of Botany, Kunming, Yunnan, China

3   Negaunee Institute for Plant Conservation Science and Action, Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL 60022 USA

4   General Zoology, Institute for Biology, Martin-Luther University Halle-Wittenberg, Hoher Weg 8, 06120 Halle (Saale), Germany

5   Cellular and Organismic Networks, Faculty of Biology, Ludwig-Maximilians-Universität München, 82152 PlaneggMartinsried, Germany

6   Hawkesbury Institute for the Environment, Western Sydney University, Hawkesbury Campus, Science Rd, Richmond NSW 2753, Australia

7   Universidade Federal dos Vales do Jequitinhonha e Mucuri (UFVJM), Faculdade Interdisciplinar em Humanidades, Curso de Licenciatura em Educação do Campo, LEC Sala 157 DEF, Campus JK, Diamantina, Minas Gerais, Brasil

8   Universidade de São Paulo, Instituto de Biociências (IB-USP), Departamento de Ecologia, São Paulo, Brasil 9University of Exeter, Environment and Sustainability Institute, Penryn Campus, University of Exeter, Penryn TR10

9   FE, UK

10   School of Life Sciences, University of Sussex, Brighton, BN1 4GE, UK

11   School of Agriculture and Food Science, University College Dublin, Dublin 2, Ireland

12   Department of Entomology, Center for Pollinator Research, Huck Institute of the Life Sciences, The Pennsylvania State University, University Park, PA 16802, USA

13   University of Oxford, Department of Zoology, South Parks Road, Oxford, OX1 3SZ

14   Department of Entomology, Millennium Science Complex, University Park, Pennsylvania State University, PA 16802, USA

15   Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacherstraße 4, 79106 Freiburg, Germany

16   Department of Natural Sciences, Manchester Metropolitan University, Chester Street, Manchester, M1 5GD, UK 17School of Applied Sciences, Edinburgh Napier University, Edinburgh, EH11 4BN, UK

18   Joseph Banks Laboratories, School of Life and Environmental Sciences, University of Lincoln, Lincoln, LN6 7TS, UK

19   Institute of Evolutionary Biology, University of Edinburgh, Ashworth Laboratories, Charlotte Auerbach Road, Edinburgh, EH9 3FL, UK

20   Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio 26, E-41092 Sevilla, Spain

21   Department of Ecological Sciences, James Hutton Institute, Aberdeen, AB15 8QH, UK

22   Grupo de Investigación Biología para la Conservación, Universidad Pedagógica y Tecnológica de Colombia, Avenida Central del Norte 39-115, 150003 Tunja, Colombia

23   Curtin University School of Molecular & Life Sciences, Kent Street, Bentley, Perth, Western Australia 6102, Australia

24   Wildlife Trust BCN, Lings House, Lings Way, Northampton NN3 8BE, UK

25   CREA Council for Agricultural Research and Agricultural Economy Analysis, Research Centre for Agriculture and Environment, Bologna, Italy

26   Departamento de Biodiversidade e Conservação da Natureza, Universidade Tecnológica Federal do Paraná, Via Rosalina Maria dos Santos 1233, CEP: 87301-899, Campo Mourão, Paraná, Brasil

27   Biodiversity Research Centre, Earth & Life Institute, UCLouvain, Louvain-la-Neuve, Belgium

28   Department of Entomology and Nematology, University of Florida, 1881 Natural Area Drive, Gainesville, FL 32611, USA

29   [home address redacted] St Helens, Merseyside, UK

30   School of Biological Sciences, Monash University, Clayton, Victoria, Australia

31   Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, Victoria, Australia

32   Plant-Insect Interactions, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

33   Department of Ecology and Animal Biology, University of Vigo, Vigo, Pontevedra, Spain

34   School of Biological Sciences, Life Sciences Building, University of Bristol, 24 Tyndall Avenue, Bristol, BS8 1TQ, UK

35   Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, Nacogdoches, Texas 75962, USA,

36   Department of Life Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK

37   Institute of Evolution and Ecology, School of Life Sciences, Central China Normal University, Wuhan, 430079 China

38   Integrated Land Management, SRUC, Auchincruive Estate, Ayr, KA6 5HW, UK

39   Université M'hamed Bougara de Boumerdes, Faculté des Sciences, Laboratoire des technologies douces, valorisation, physico-chimie des matériaux biologiques et biodiversité, 1 Avenue de l'Indépendance 35000 Boumerdes, Algeria

40   Department of Animal and Plant Science, The University of Sheffield, Western Bank, S10 2TN, UK

41   Department of Environmental Sciences, Western Norway University of Applied Sciences, P.O. Box 133, NO-6851 Sogndal, Norway

42   Department of Agricultural, Forest and Food Sciences, Università degli Studi di Torino, Largo Paolo Braccini, 10095, Turin, Italy

43   Department of Plant Sciences, University of Oxford, South Parks Road, Oxford, OX1 3RB, UK

44   University of Ulm, Institute of Evolutionary Ecology and Conservation Genomics, Albert-Einstein-Allee 11, 89081 Ulm, Germany

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45   University of Würzburg, Department of Animal Ecology and Tropical Biology, Biocenter, Am Hubland, 97074 Würzburg, Germany

46   [home address redacted] Ashton Under Lyne, Greater Manchester, UK

47   Department of Plant and Crops, Faculty of Bioscience Engineering, Ghent University, Ghent, Belgium

48   School of Biological Sciences, University of Portsmouth, Portsmouth PO1 2DY, UK

49   Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA

50   Sussex Biodiversity Record Centre, Woods Mill, Shoreham Rd, Henfield BN5 9SD, UK

51   Département d'Agronomie, Faculté des Sciences, Laboratoire de Bioinformatique, Microbiologie Appliquée et Biomolécules (BMAB), Université M'Hamed Bougara de Boumerdès, Algérie

52   Steven Falk: [home address redacted] Kenilworth, Warwickshire, UK

53   School of Ecosystem and Forest Sciences, University of Melbourne, Parkville 3010, Australia

54   Centre for Agroecology, Water and Resilience (CAWR) Coventry University, Ryton Organic Gardens, Coventry, CV8 3LG, UK

55   UK Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Wallingford, OX10 8BB, UK

56   University of East Anglia, Norwich Research Park, Norwich, NR4 7TJ, UK

57   School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK

58   Department of Health Studies, School of Life Sciences and the Environment, Royal Holloway, University of London Egham, Surrey, TW20 0EX, UK

59   Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Università di Bologna, via Irnerio 42, Bologna, Italy

60   Sustainability Research Institute (SRI), University of East London, Knowledge Dock Building, Docklands Campus, 4-6 University Way, London E16 2RD, UK

61 Dutch Butterfly Conservation, Mennonietenweg 10, 6702 AD Wageningen, The Netherlands

62 Laboratório de Polinização, Reprodução e Fenologia de Plantas (LPRF)/InBio, Universidade Federal de Mato Grosso do Sul, Campo Grande/MS, Brazil

63   Agroecology Lab CP 264/02, Université libre de Bruxelles (ULB), Av. FD Roosevelt 50, B-1050 Brussels, Belgium

64   Nature Conservation and Landscape Ecology, Albert-Ludwigs-University Freiburg, Tennenbacher Str. 4, 79106 Freiburg, Germany

65   Department of Geography and Environmental Sciences, Ellison Building, Northumbria University, Newcastle upon Tyne, NE1 8ST, UK

66   Natural Resources Institute, University of Greenwich, Chatham Maritime, Kent, ME4 4TB, UK 67Nelson Mandela African Institution of Science and Technology, Arusha, Tanzania

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Conclusions

This research improved knowledge on the biology of the relatively recent exotic bee *M. sculpturalis* in Europe and the potential negative impacts associated with its nesting behavior. The findings are relevant for the understanding of the ecological invasion displayed by a generalist pollinator. The study unveils a potential combining effect of direct (eviction) and indirect competition (emergence blocking) acting at different times on the nests of *Osmia* bees. However, extended sampling effort could help to draw more conclusive understanding on the impacts of this alien species. Untill now, control measures that have been suggested are based on the monitoring of potential distribution, nest-trapping and nest removal (Lanner et al., 2021; Ruzzier, et al., 2020). More research on the factors affecting population dynamics of its spread is needed to develop an effective practical intervention.

The understandings and results obtained in this PhD work provide useful information to assess the potential impact of pollen diets on development, and therefore, the survival of the offspring. Moreover, this work has highlighted that the main strategy of nesting females to promote the survival of the progeny is to provide pollen from an abundant main pollen source, instead of diversifying proportionally with different pollen sources. However, additional replication is needed, and conclusions cannot be drawn from the limited number of pollen samples collected thus far. The two species of *Osmia* studied have different pollen preferences even when their nesting sites and nesting periods overlapped.

The present study provides evidence that pollen diet is not always a determinant factor affecting the development of larvae of solitary bees. Immature, progeny had pollen mixtures very similar compared with the well-developed offspring. Similar results were obtained by Tobajas et al. (2022) and suggest that polylecty in bees might also have evolved as an foraging strategy from a dependence on main pollen sources that could be complemented by other nutritional plant species. We did not find evidence of females being able to allocate targeted pollen

mixing to optimize food quality for their progeny. The effect of pollen mixture to maximize development remains to be investigated in depth.

Since monitoring pollinator interactions with conventional methods in ecological settings became logistically difficult in a pandemic context, part of this research focused on the participation on monitoring activities in a feasible context of scientific collaboration using private gardens and public areas that could be considered "less wild", but of a greater interest due to the standard methods used and the future research questions that can be addressed.

On the other hand, this study is in agreement with the increased public interest on nature found during COVID lockdowns (Roll et al., 2021). Trained ecologists observing and recording the biodiversity interacting in their vicinity and using common methods, may create important datasets of reference for the present and future monitoring activities of wider society groups, for instance, citizens interested on pollinator conservation.

Overall, this study has progressed understanding in the importance of the identification skills and coordinated monitoring activities for the development of global databases. With predicted pollinators decline, the use of common and standardized data will become crucial to promote common recommendations for management practices in gardens and policy action for improving pollinator habitats.

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