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Use of human-made nesting structures by wild bees in an urban environment

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Abstract Most bees display an array of strategies for building their nests, and the availability of nesting resources plays a significant role in organizing bee communities. Although urbanization can cause local species extinction, many bee species persist in urbanized areas. We studied the response of a bee community to winter-installed human-made nesting structures (bee hotels and soil squares, i.e. 0.5 m deep holes filled with soil) in urbanized sites. We investigated the colonization pattern of these structures over two consecutive years to evaluate the effect of age and the type of substrates (e.g. logs, stems) provided on colonization. Overall, we collected 54 species. In the hotels, two gregarious species, *Osmia bicornis* L. and *O. cornuta* Latr. dominated the community (over 87 % of the data). Over 2 years, the age of the soil squares did not affect their level of colonization and the same was true for the hotels with respect to *O. bicornis* and 'other species'. However, *O. cornuta* occurred less often and raised fewer descendants in 1-year old hotels than in new ones. Bee nesting was not affected by the soil texture and, among above-ground nesting bees, only

O. bicornis showed a preference for some substrates, namely *Acer* sp. and *Catalpa* sp. In a context of increasing urbanization and declining bee populations, much attention has focused upon improving the floral resources available for bees, while little effort has been paid to nesting resources. Our results indicate that, in addition to floral availability, nesting resources should be taken into account in the development of urban green areas to promote a diverse bee community.

Introduction

Bees (Hymenoptera: Anthophila) display an array of strategies regarding the habitat they nest in, the type of substrate they use, and the materials they require for their nest construction (Potts et al. 2005). Bees can be classified into three guilds on the basis of their nesting habits (O'Toole and Raw 2004): ground or above-ground nesting and cleptoparasites. Ground nesting bees, represent the majority of bee species and dominate in many open habitats (O'Toole and Raw 2004; Michener 2007). Ground nesting female bees excavate subterranean tunnels terminated by chambers or cells, which they provision with a mass of pollen and nectar (Cane 1991). All species of Andrenidae and Melittidae are ground-nesting, as are most species of Halictidae and Colletidae (Michener 2007). The above-ground nesting guild, which is dominated by Megachildae and Apidae families, nest either in pre-existing holes (Roubik 1989; Michener 2007) or dig their

This work is dedicated *in memoriam* of Robert Fonfria.

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own cavities in firm substrate (e.g. pithy plant stems or soft wood; Roubik 1989; Michener 2007). Some species, called gregarious nesters [e.g. *Osmia bicornis* Linné (Fliszkiewicz et al. 2013) or *Andrena vaga* Panzer (Rezkova et al. 2011)], breed individually like solitary bees, but nest close to conspecifics, sometimes at high densities over a limited area. Finally, cleptoparasitic bees do not construct nests, but instead lay their eggs in the nests of other bees so that these eggs can hatch and steal the food and the nest, and are therefore referred to as cuckoo bees (Wcislo 1987).

Little is known about particular biotic and abiotic factors influencing nesting success or nesting site selection by different bee species (Cane 2008; Sardiñas and Kremen 2014). A range of studies point out that within-site characteristics, such as exposed bare ground (e.g. Potts et al. 2005), litter cover (e.g. Grundel et al. 2010), soil texture (e.g. Cane 1991), soil compaction (e.g. Wuellner 1999; Sardiñas and Kremen 2014), soil moisture (e.g. Wuellner 1999), soil slope (e.g. Potts and Willmer 1997; Sardiñas and Kremen 2014), spatial distribution (e.g. Sardiñas and Kremen 2014), or number of potential nesting cavities (cracks or holes in the ground; e.g. Potts et al. 2005), were determinants in nest selection of ground-nesting bees. Above-ground nesting bees nest in different types of substrate such as wood, hollow plant stems (e.g., *Phyllostachys* sp., *Phragmites* sp., or *Arundo* sp.), pithy plant stems (e.g., *Buddleja* sp., *Rubus* sp., or *Ailanthus* sp.), or any other sort of cavities (e.g., in adobe walls, abandoned insect burrows, bird nests or even snail shells) (Amiet et al. 1999; Pouvreau 2004; Michener 2007). The diameter and height of pre-existing holes plays an important role in nesting site selection (e.g. Scott 1994). Bees also need different materials to build their nest. For example, *Osmia* spp., use mud to separate cells and close their nest and *Heriades truncorum* uses some resin (Amiet et al. 2004; Michener 2007).

Two studies provide quantitative evidence showing that nesting resources have an important role in structuring bee communities (Potts et al. 2003) or key guilds within communities (Cane 1991). Potts et al. (2003) examined 14 habitat characteristics as predictors of bee community structure. Floral characters were the primary determinants, but still 5 % of the bee community structure was explained by the diversity of nesting resources available, and this went up to 10 % when only dominant bee species were considered. These findings demonstrate that the availability of diverse nesting resources plays a significant role in organizing bee communities. Habitats may not be uniform in their ability to support populations of bees in relation to the nesting sites available (Grundel et al. 2010). Urbanization is one of the principal causes of species extirpation, threatening species by the direct destruction of their habitat and also indirectly by removing their resources (Czech et al.

2000; Zanette et al. 2005; Hennig and Ghazoul 2012). In the course of urbanization, impervious surface modifies habitats (Marzluff and Ewing 2001), and usually, the open green spaces left in urban areas are often parks, gardens, brownfields, train corridors, and recreational areas (Müller et al. 2013). The soils of these remaining areas are modified and their management changes the food and nesting resources available to bees compared to more natural environment (Cane et al. 2006; Müller and Werner 2010; Hennig and Ghazoul 2012). Thus urbanization often degrades nesting habitat, especially for ground-nesting bees, by transforming vegetation composition and structure (e.g. scrub converted to grass lawns, washes confined to concrete flumes) and altering surface soils through compaction (Cane et al. 2006). Cutting dead trees or removing fallen trees and brush piles in urban areas make these potential nesting sites no longer available as substrates for bees to nest in (Steffan-Dewenter and Leschke 2003; McFrederick and LeBuhn 2006). Changes due to urban management are not as adverse for above-ground nesting bee species as for ground-nesting species, because cavities in wood and other substrates also occur in the houses, fences, and introduced woody landscape vegetation (Cane et al. 2006). Nevertheless, cutting dead trees or removing fallen trees and brush piles in urban areas removes potential nesting sites for bees (Steffan-Dewenter and Leschke 2003; McFrederick and LeBuhn 2006). Also, landscaping with horticultural taxa (Garbuzov and Ratnieks 2014) and the spread of invasive plants (Meekins and McCarthy 2001) leads to a loss of native vegetation. Indeed, oligolectic bee species (i.e. depending exclusively on one or a few plant taxa for pollen food) are more rare in urban areas than polylectic bee species (i.e. capable of gathering pollen from a broad array of plant species) (Fetridge et al. 2008; Banaszak-Cibicka and Żmihorski 2012) because the latter are capable of gathering pollen from exotic ornamental plants (Frankie et al. 2005). Yet, despite all this, many bee species can persist in urbanized areas (McFrederick and LeBuhn 2006; Banaszak-Cibicka and Żmihorski 2012; Fortel et al. 2014).

Ground-nesting bees can be assessed using tent traps that cover a portion of the ground, known as emergence traps (e-traps), and bee-hotels (usually made from bundled plant stems or holes drilled in wood) can artificially aggregate nesting sites above densities naturally available for above-ground nesting bees (Krombein and Wasps 1967). But these methods have rarely been used (Kim et al. 2006; MacIvor and Packer 2015). Standard bee collection techniques are pan-traps (colored bowls filled with soapy water) and hand netting at flowers (Westphal et al. 2008), but these methods do not directly capture bees from their nests. Therefore, the ability of habitat to support nesting is often inferred from the presence of bee species from specific nesting guilds (e.g.

Morandin and Kremen 2013), assuming that bees found at a location must be nesting somewhere within a distance corresponding to their foraging range (Lonsdorf et al. 2009), or the presence of potential nesting resources (e.g. Potts et al. 2005; Grundel et al. 2010), assuming that the availability of nesting resources affects the ability of native bees to nest in a given area.

Since nesting availability plays a role in structuring bee communities (Cane 1991; Potts et al. 2003), we reasoned that providing human-made nesting structures in the urban environment may be a useful tool to study bee communities and possibly locally sustain and increase the population of a range of species. In this context, we studied, over a 2-year period, how human-made nesting structures (bee hotels and soil squares) can be useful for the bee community in an urban environment. Our hypotheses were that (1) the abundance of ground and above-ground nesting bees would increase in the bee hotels and the soil squares, respectively, between the first and the second year of installation, (2) the age of nesting structures would have a positive effect on abundance and diversity of nesting bee species; (3) some substrates (i.e. logs, stems, or soil) would be preferred to others by bees for building their nests.

Materials and methods

Study sites

The study was conducted in the urban community of Grand Lyon, France, which includes 58 towns around Lyon (45°46′N, 4°50′E) and covers an area of 516 km^2 with approximately 1.3 million inhabitants (Insee Rhône-Alpes 2013). The climate of Lyon is at the temperate-Mediterranean interface. The 30-year annual average temperature is 12 °C with a minimum of 3 °C in January and a maximum of 21 °C in July (InfoClimat 2011).

The sites studied here are a subset from those studied in Fortel et al. (2014). We selected 16 sites with more than 30 % of impervious surface (i.e. buildings, roads and industrial areas) over a two km radius. Eight sites had a proportion of impervious surface between 30 and 70 % (periurban sites), and the remaining eight had >70 % of impervious surface (urban sites). Each site was located in green areas, parks or gardens. All sites were separated by less than two km from each other to prevent overlapping of bee communities (Zurbuchen et al. 2010b). Indeed, wild bees cover relatively short foraging or commuting flights, most often one to several hundred meters long (Zurbuchen et al. 2010a, b), and the capability to cover long distances and to use resources on a large spatial scale mostly applies to larger bees (e.g. genera *Bombus* or *Xylocopa*; Greenleaf et al. 2007).

Human-made nesting structures

Soil squares and bee hotels were built to study the use and preference of wild bees with respect to each artificial nest type (Fig. 1).

Each soil square consisted of a 1 m^2 wooden frame surrounding a 0.5 m deep hole with a layer of stones at the bottom to provide drainage. The soil squares were located on flat ground and in open areas as much as possible so as to be exposed to direct sun as soil exposition is important for nest site selection (Wuellner 1999; Potts et al. 2005). Squares were dug and filled with the local soil alone (3 control squares) or with this soil mixed with 1/4, 1/3 or 1/2 of clay or sand. We then had three groups of soil squares: one group with one soil square with 100 % of local site (the one excavated from the holes), one with 3/4 of local soil and 1/4 of sand and one with 3/4 of local soil and 1/4 of clay, a second group with one soil square with 100 % of local site (the one excavated from the holes), one with 2/3 of local soil and 1/3 of sand and one with 2/3 of local soil and 1/3 of clay and a third group with one soil square with 100 % of local site (the one excavated from the holes), one with 1/2 of local soil and 1/2 of sand and one with 1/2 of local soil and 1/2 of clay. Plant growth within soil squares was removed manually on a monthly basis to maintain areas of bare soil that are essential for soil-nesting bees (Potts et al. 2005). This frequency was also chosen to minimize damage to the potential nests already built. Squares were covered with a frame of chicken wire so that domestic animals would not damage the device or disturb the nesting activity.

Bee hotels were set-up near the soil squares. At each site, we built three hotels oriented in different directions (e.g. north/west-south/east). They consisted of 4 × 2 m wooden structures with 9 compartments measuring 0.8 m wide × 0.45 m high × 0.5 m deep and filled with various types of nesting materials known to be used by above-ground nesting bees, such as logs drilled with holes, hollow or pithy stems of different species. Overall four compartments contained logs or stems while the other ones contained adobe. We used, eight species of logs (*Acer* sp., *Ailanthus* sp., *Fraxinus* sp., *Platanus sp.*, *Populus* sp., *Prunus* sp., *Robinia* sp, and *Tilia* sp.), three of hollow stems (*Arundo* sp., *Phragmites* sp, and *Phyllostachys* sp.), and four of pithy stems (*Ailanthus* sp., *Catalpa* sp., *Buddleja* sp, and *Sambucus* sp.). Inasmuch as possible, we used materials available where the hotels were located (remnants from tree pruning and hedge trimmings). The logs were drilled with electric drills on both ends with holes ranging from 4 to 12 mm diameter and their depth was 0.20 m to avoid drilling throughout. Every compartment was completely filled in order to have a large and potentially non-limiting number of cavities.

At each site, nine soil squares and three bee hotels were built. Eight sites (four periurban and four urban, selected at

Fig. 1 Human-made nesting structures set in the winter of 2010/2011 in Sainte-Foy-Lès Lyon, France. A nine-compartment bee hotel is on the left while three soil squares are visible on the right

random within the eight periurban sites and the eight urban sites respectively) were set up during *Year 1* (winter of 2010/2011) and the eight remaining during *Year 2* (winter of 2011/2012). With the data from the eight sites used in *Year 1*, we were able to compare the nesting over 2 years without any site effect and with the data from *Year 2* over the 16 sites we were able to compare old and new nesting structures without inter-annual climate fluctuations.

Nesting activity monitoring

Nesting activity in square soils

To sample soil-nesting bees, a net cage of 0.36 × 0.61 m was placed over a corner of each square for a 45 min period on a monthly basis from March to September in 2012 and 2013. Since the activity of bee species depends on temperature and day period (e.g. Corbet et al. 1993; Stone et al. 1999; Gottlieb et al. 2005), alternate morning or afternoon samplings were performed only during periods of good weather for foraging activity (maximum temperature ≥15 °C, sky sunny or with scattered clouds only, and wind speed ≤15 km/h; Westphal et al. 2008). The corners of the soil squares for net cage placement were randomly chosen at the beginning of the season for each square, and then sampled repeatedly without changes throughout the season. The corners were different in 2012 and in 2013. Bees were captured either in the cage, trying to get out of their nest, or

nearby the outside of the cage with a net, when trying to come back into their nest. In the winter 2012, we collected a composite sample of 100 g of soil representative of the soil volume in each square and the granulometric composition of these samples was analyzed using standard methodology (National Soil Analysis Laboratory, INRA Arras). The percentages of clay, silt and sand on a weight basis were used to locate the soil of each square into the discrete categories of a soil texture triangle (U. S. Department of Agriculture 1951). We used R package plotrix to represent the distribution of soil squares in the texture triangle (Lemon 2006; see Supplementary Methods 1).

Nesting activity in bee hotels

To make sure that bees were in diapause, we took out an eighth of each type of hotel nesting substrate in each compartment of each hotel at each site after the first winter frost. For the stems, we divided the surface of each compartment in eight parts of 0.2 × 0.23 m and took out the elements of one of them (chosen randomly) each winter using a custom-made metallic frame that we pushed amidst the stems. For the logs, we first counted the total number of holes in the logs of each species and then took out logs containing about one eighth of this total number of holes. Each sample of log or stem was put into a net cage of 0.36 × 0.36 × 0.61 m (Bioquip, CA, USA). These cages were placed under a screen tunnel so that bees could

emerge in the cages all year long. Bees that emerged were collected from the cages on a weekly basis from March to September. Each emergence cage contained logs or stems removed from a single compartment of a hotel. After the removal of each log or stem sample in a compartment, we replaced it with logs or stems of the same species. For each species of material in each compartment, bee occurrence was 1 if there was at least one individual of the bee species considered that emerged from the material, and 0 otherwise, meaning the absence of bee. Abundance was the number of specimens of the bee species considered that emerged from the sample of material and we calculated an *emergence rate* corresponding to the ratio between the number of emerged bees and the number of holes in the logs or stems.

All the specimens of bee which were collected from the soil squares or the emergence cages were frozen for later processing. Individuals were then pinned, labeled, identified to genus, and sent for identification to species to the respective authority for each genus (see Acknowledgements). All voucher specimens are now deposited in the bee collection of INRA Avignon. For the taxonomy, we followed the nomenclature of Kuhlmann et al. (2013).

Data analyses

As human-made nesting structures were put in place over 2 years, we conducted diachronic (relating to the changes in the data base that happen over the 2 years) and synchronic (relating to differences between two data base obtained the same year) analyses of the species occurrence and abundance data. First, we analyzed the bees that emerged from the nesting elements of the hotels built in *Year 1* in the 2 years that followed their set-up (2012 and 2013; diachronic approach). The same sampling schedule was used for the soil squares set-up in *Year 1*. This first approach was used to evaluate the colonization pattern over the two seasons in the same structures. Second, we investigated the influence of the age of the nesting materials that was put in place in *Year 1 or Year 2* by scoring the emergence that took place over 2013 in all sites (synchronic approach). Combining the two approaches enabled us to test if the age of a nesting structure had a positive or negative influence on its colonization by bees, or if the colonization pattern was more an effect of a particular season. As the data were zero inflated, in subsequent analyses, linear mixed-effects models were used with *occurrence* (0–1 binary data) and *abundance* (counts; zero excluded) as dependent variables, while *year of sampling* or *year of construction* was the main fixed effect factor. As all sites were different and so were the hotels and composition of the soil squares, we added *site, soil square* and *texture of soil* for the analyses of soil squares recordings,

and *site, bee hotel* and *material species* as random effect factors for the analyses of emergence data from bee hotels. In the analyses of emergence data from bee hotels, we separated bees into three groups (*Osmia cornuta* (Latreill), *O. bicornis*(Linné) and 'other species'), because *O. cornuta* and *O. bicornis* made over 87 % of the emerging specimens and we analyzed the data separately for each of the three groups.

We also performed linear mixed-effects models to test the effect of either the types of logs or stems in the hotels or the *soil texture* in the squares on bee *species richness* for soil squares and *emergence rate* for bee hotels (dependent variables). Random effect factors were the *year of construction* and *year of sampling* combination, and *site*. Post-hoc Tukey tests were done on bee *species richness* for soil squares and *emergence rate* for bee hotels to estimate the differences among soil texture classes for the soil squares and logs and hollow stems and pithy stems in bee hotels.

All models were run using lme4 (Bates et al. 2011) and nlme (Pinheiro et al. 2010) packages in R version 3.2.2 (R Core Team 2015). Post-hoc Tukey tests were computed using multcomp package in R (Hothorn et al. 2008). For the diachronic and synchronic analyses, we used a threefold Bonferroni correction for all models on the three groups of species (Rice 1989).

For the analyses, we took 14 (87.5 % of the total number of studied sites) and 15 (93.75 %) sites into account for soil squares and bee hotels, respectively, because all logs and stems had been stolen from the bee hotels on one site and the square soils of two sites were not built soon enough to take them into account.

Results

First of all, we collected bees at all 16 sites of our study on both soil squares and bee hotels. Furthermore, our dataset is a subsample because we only sampled at random 1/4th of each soil square and 1/8th of the total number of cavities of each type of nesting substrate in each compartment at each site. So, by extrapolation we could expect to have four times as many bees that nested in the soil squares (i.e. 232) and eight times as many bees that emerged from the hotels (i.e. 3102), that is about 1,000 and 25,000 bees, respectively.

Wild bee fauna in the nesting structures

Soil squares

Over the 2 years of sampling, we collected 232 specimens (97 in 2012 and 135 in 2013) belonging to 37 species (23 in 2012 and 31 in 2013) in the soil squares (Table 1). An average of 5.14 bee specimens per site were collected in

Table 1 List of the species collected in the human-made nesting structures

Emergence from bee hotel

Taxon	Family	Number of specimens in 2012	Number of specimens in 2013
Anthidium florentinum (Fabricius)	Megachilidae	12	0
Chelostoma florisomne (Linnaeus)	Megachilidae	11	65
Heriades crenulatus Nylander	Megachilidae	15	0
Heriades truncorum (Linnaeus)	Megachilidae	122	21
Hoplitis adunca (Panzer)	Apidae	2	5
Hylaeus communis Nylander	Colletidae	8	1
Hylaeus incongruus Förster	Colletidae	1	0
Megachile centuncularis (Linnaeus)	Megachilidae	5	0
Megachile rotundata (Fabricius)	Megachilidae	1	0
Megachile sculpturalis Smith	Megachilidae	0	16
Megachile versicolor Smith	Megachilidae	0	12
Osmia bicornis (Linnaeus)	Megachilidae	298	535
Osmia brevicornis (Fabricius)	Megachilidae	0	3
Osmia caerulescens (Linnaeus)	Megachilidae	54	9
Osmia cornuta (Latreille)	Megachilidae	426	1450
Osmia melanogaster Spinola	Megachilidae	1	0
Osmia submicans Morawitz	Megachilidae	12	4
Osmia tricornis Latreille	Megachilidae	1	0
Stelis breviuscula Nylander (C)	Megachilidae	0	1
Stelis minuta Lepeletier and Audinet-Serville (C)	Megachilidae	8	0
Xylocopa violacea (Linnaeus)	Apidae	1	2
Total		978	2124
Total		3102	

Captures in soil squares

Taxon	Family	Number of specimens in 2012	Number of specimens in 2013
Andrena dorsata (Kirby)	Andrenidae	1	0
Andrena flavipes Panzer	Andrenidae	0	1
Andrena florea Fabricius	Andrenidae	0	1
Andrena gravida Imhoff	Andrenidae	0	1
Andrena minutula (Kirby)	Andrenidae	1	3
Andrena minutuloides Perkins	Andrenidae	2	1
Andrena simontornyella Noskiewicz	Andrenidae	1	2
Andrena viridescens Viereck	Andrenidae	0	1
Halictus subauratus (Rossi)	Halictidae	14	31
Halictus tumulorum (Linnaeus)	Halictidae	0	2
Hoplitis adunca (Panzer)	Apidae	0	1
Hoplitis ravouxi (Pérez)	Apidae	0	1
Lasioglossum fulvicorne (Kirby)	Halictidae	1	0
Lasioglossum griseolum (Morawitz)	Halictidae	0	2
Lasioglossum laticeps (Schenck)	Halictidae	1	1
Lasioglossum leucozonium (Schrank)	Halictidae	1	2
Lasioglossum malachurum (Kirby)	Halictidae	3	1
Lasioglossum mesosclerum (Pérez)	Halictidae	0	1
Lasioglossum minutissimum (Kirby)	Halictidae	5	12
Lasioglossum morio (Fabricius)	Halictidae	12	24
Lasioglossum pallens (Brullé)	Halictidae	0	1

Table 1 continued

Captures in soil squares			
Taxon	Family	Number of specimens in 2012	Number of specimens in 2013
Lasioglossum pauxillum (Schenck)	Halictidae	24	9
Lasioglossum politum (Schenck)	Halictidae	6	15
Lasioglossum punctatissimum (Schenck)	Halictidae	0	3
Lasioglossum pygmaeum (Schenck)	Halictidae	3	1
Lasioglossum semilucens (Alfken)	Halictidae	1	4
Lasioglossum villosulum (Kirby)	Halictidae	13	6
Lasioglossum zonulum (Smith)	Halictidae	1	0
Megachile pilidens Alfken	Megachilidae	0	2
Nomada atroscutellaris Strand (C)	Apidae	0	1
Nomada bifasciata Olivier (C)	Apidae	1	0
Nomada flavoguttata (Kirby) (C)	Apidae	2	1
Osmia caerulescens (Linnaeus)	Megachilidae	0	2
Osmia submicans Morawitz	Megachilidae	0	2
Sphecodes croaticus Meyer (C)	Halictidae	1	0
Sphecodes ephippius (Linné) (C)	Halictidae	1	0
Sphecodes longulus Hagens (C)	Halictidae	2	0
Total		97	135
Total		232	

(C) Cleptoparasitic bee species

The species collected in both soil squares and bee hotels is in bolt

2012 (with a minimum of 0 and a maximum of 20) and 9.64 in 2013 (with a minimum of 1 and a maximum of 38). The most abundant species was *Halictus subauratus* (Rossi; 19.4 % of the total number of specimens), which is a non-solitary bee species, which is also the case for the three next most abundant species (*Lasioglossum. morio* (Fabricius; 15.5 %), *L. pauxillum* (Schenck; 14.2 %) and *L. politum* (Schenck; 9.1 %)). Six species were cleptoparasites (Apidea: *Nomada atroscutellaris* Strand, *N. bifasciata* Olivier, *N. flavoguttata* (Kirby) and Halictidae: *Sphecodes croaticus* Meyer, *S. ephippius* (Linné), and *S. longulus* Hagens), which represents 16.2 % of the total number of species. We recorded 15 species as singletons that is 40 % of the total number of species.

Bee hotels

We collected 3,102 specimens (978 in 2012 and 2,124 in 2013) belonging to 21 species (18 in 2012 and 14 in 2013) over the 2 years in the bee hotels (Table 1). An average of 122.25 bee specimens were collected per site in 2012 (with a minimum of 34 and a maximum of 191) and 132.75 in 2013 (with a minimum of 1 and a maximum of 410). The most abundant species were *Osmia cornuta* (60 % of the total number of specimens), and *O. bicornis* (27 %), which are both gregarious species. They were collected on all 16 sites. Two species were cleptoparasites (Megachilidae: *Stelis breviuscula* Nylander and *S. minuta* Lepeletier and Audinet-Serville), which represents 9.5 % of the total number of species. We recorded only five species as singletons, i.e. 24 % of the species list. The first emergence was recorded on the 20th of March in 2012 and the 13th of March in 2013 and the last one on the 24th of July in 2012 and on the 12th of August in 2013. The emergences of *O. cornuta* were recorded between the 20th of March and the 26th of June in 2012 and between the 13th of March and the 17th of May in 2013 and between the 24th of March and the 3rd of July in 2012 and between the 13th of March and the 17th of May in 2013 for *O. bicornis*.

Evolution of colonization over time (diachronic analyses)

Soil squares

In the soil squares installed in *Year 1*, both the occurrence and abundance of wild bees remained similar over the 2 years of sampling (Table 2; Fig. 2a, b).

Table 2 Pairwise comparisons of the occurrence frequencies and abundance of bee groups during the year of sampling or the year of structure installation

Model	Dependent variable	Nesting site type	Bee group	Estimate ± SE	z-value	p
Diachronic analyses: 2012 vs 2013 samples	Occurrence frequency	Bee hotels	Other species	−1.67 ± 0.35	−4.73	<0.001*
			Osmia bicornis	−1.02 ± 0.31	−3.26	0.0011*
			Osmia cornuta	1.31 ± 0.32	4.15	<0.001*
		Soil squares		0.57 ± 0.38	1.52	0.13
	Abundance	Bee hotels	Other species	0.01 ± 0.26	0.04	0.97
			O. bicornis	0.65 ± 0.26	2.45	0.037
			O. cornuta	0.45 ± 0.2	2.25	0.032
		Soil squares		0.12 ± 0.11	1.16	0.26
Synchronic analyses: Installation in 2010/2011 vs 2011/2012	Occurrence frequency	Bee hotels	Other species	0.62 ± 0.52	1.2	0.23
			O. bicornis	−5.1 ± 2.9	−1.76	0.078
			O. cornuta	−1.61 ± 0.47	−3.41	<0.001*
		Soil squares		−0.5 ± 0.7	−0.72	0.47
	Abundance	Bee hotels	Other species	0.075 ± 0.39	0.19	0.85
			O. bicornis	−0.73 ± 0.58	−1.26	0.24
			O. cornuta	−1.13 ± 0.38	−2.96	0.012*
		Soil squares		−0.23 ± 0.14	−1.69	0.12

Significance was calculated after the Bonferroni correction (i.e., $p \times 3$) and is marked with an * when $p < 0.016$ (See Figs. 2 and 3 for graphical representations)

Fig. 2 Changes over time of the bee captures in soil squares over two consecutive seasons after their installation in the winter of 2010/2011 (**a** and **b**) and effect of the age of the soil squares on the bee captures recorded in 2013 (**c** and **d**). The *symbol* and the *horizontal bar* above each pair of columns indicate the significance of the difference between these years (NS: $p > 0.05$. See Table 2 for detailed statistics)
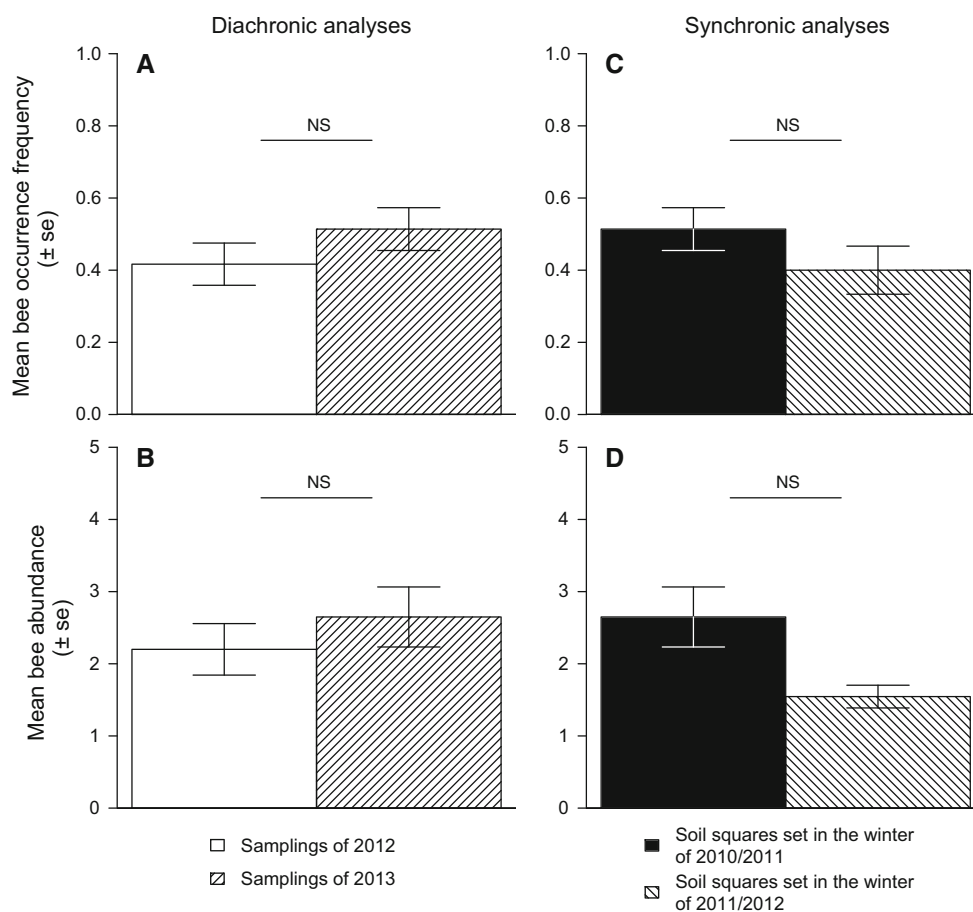
Fig. 3 Changes over time of the bee captures in bee hotels over two consecutive seasons after their installation in the winter of 2010/2011 (**a** and **b**) and effect of the age of the material in bee hotels on the bee captures recorded in 2013 (**c** and **d**). The *symbol* and the *horizontal bar* above each pair of columns indicate the significance of the difference between the years (NS: $p > 0.05$; *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$. See Table 2 for detailed statistics)
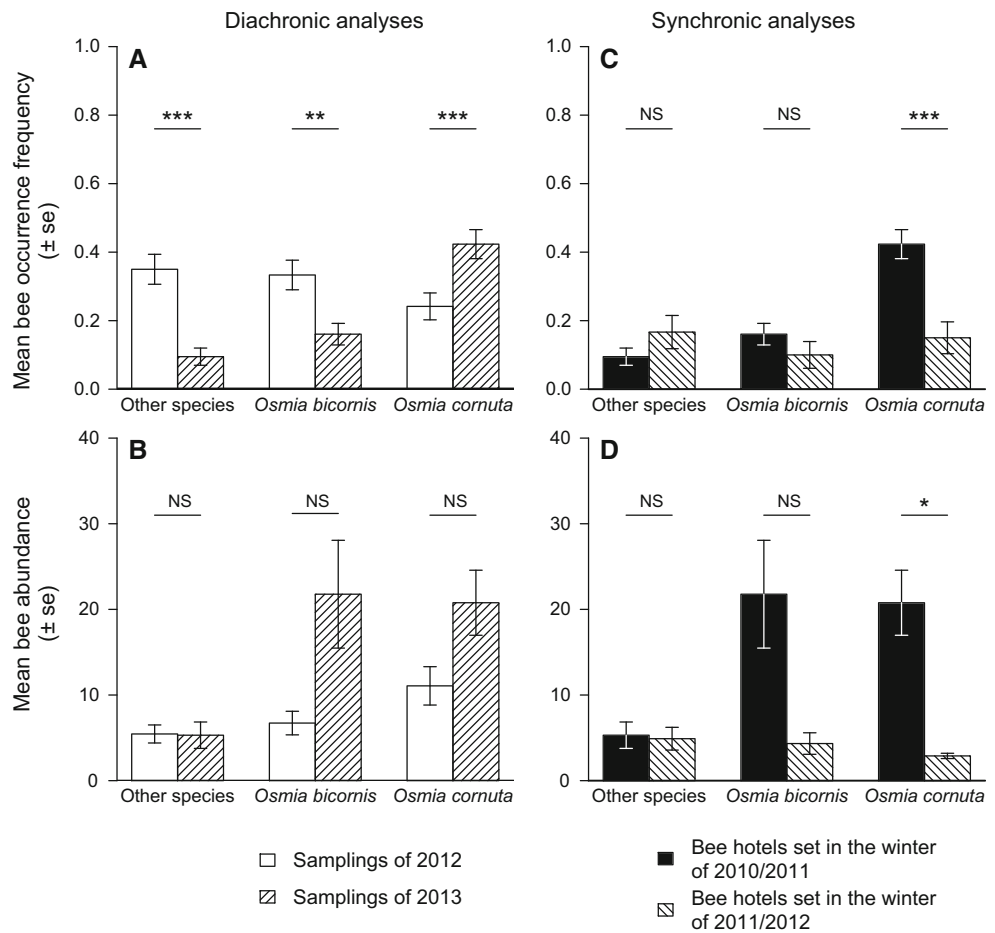
Bee hotels

In the bee hotels installed in *Year 1*, the occurrence of each of the three groups was different between the first and second year. *Osmia bicornis* and 'other species' were significantly less frequent in 2013 than in 2012, but the opposite was true for *O. cornuta* (Table 2; Fig. 3a). The abundance of the three groups of species was similar over the 2 years (Table 2; Fig. 3b).

Influence of the age of nesting structures (synchronic analyses)

Soil squares

In 2013, neither the occurrence nor the abundance of wild bees was different between the squares built up in *Year 1* and those built in *Year 2* (i.e., 1-year old soil squares compared to new ones; Table 2; Fig. 2c, d).

Bee hotels

Neither the occurrence nor the abundance of both 'other species' and *O. bicornis* were different between the hotels installed in *Year 1* and those installed in *Year 2* (Figs. 3a, d). However, both the occurrence and the abundance of *O. cornuta* were lower in the 1-year old hotels than in the new ones (Table 2; Figs. 3c, d).

Effect of nesting substrates

Soil squares

The soils of our 126 squares (corresponding to 9 squares on each of the 14 sites of the study) fell into six categories in the triangle of soil texture (two clay, three clay-loam, 32 loam, 22 loamy-sand, nine sandy-clay-loam, and 58 sandy-loam: see Supplementary Methods 1). Soil texture did not affect the species richness nor on the abundance ($F_{4,246} = 1.49$, $p = 0.2$ and $F_{4,246} = 0.62$, $p = 0.64$).
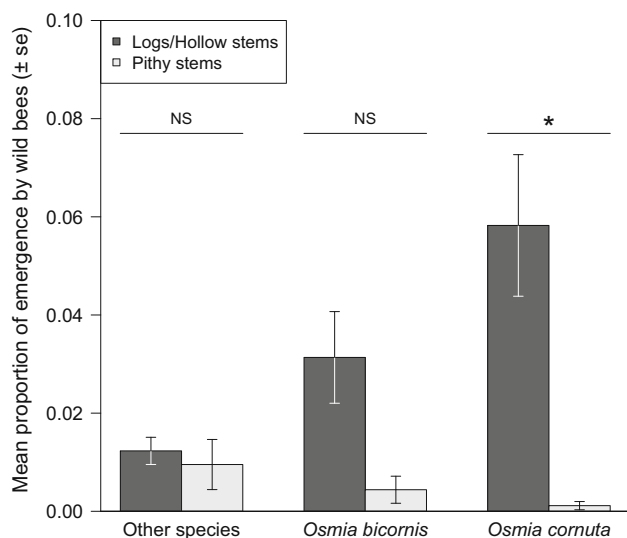
Fig. 4 Mean proportion of emergence rate of wild bees in logs and hollow stems compared to pithy stems. The *symbol* and the *horizontal bar* above each pair of columns indicate the significance of the difference between the years (NS: $p > 0.05$; *: $p \leq 0.05$)

Bee hotels

Both *O. bicornis* and *O. cornuta* nested in holes in logs and hollow stems as well as in pithy stems. The emergence rates of *O. bicornis* and 'other species' were similar in the two categories of substrate, whereas the emergence rate of *O. cornuta* was higher in logs or hollow stems than in pithy stems (Fig. 4). Within each of the two categories of substrate, the emergence rates of *O. cornuta* and of 'other species' were similar among the holes in the eight species of logs and the three species of hollow stems ($F_{10,191} = 0.66$, $p = 0.76$ and $F_{10,191} = 0.97$, $p = 0.47$ for *O. cornuta* and 'other species', respectively). This was also the case among the four species of pithy stems ($F_{3,50} = 0.84$, $p = 0.48$ and $F_{3,50} = 0.6$, $p = 0.62$ for *O. cornuta* and 'other species', respectively). However, the substrate species had a significant effect on the emergence rate of *O. bicornis*, for both groups of substrates ($F_{10,191} = 2.61$, $p = 0.0054$ for logs and hollow stems and $F_{3,50} = 6.08$, $p = 0.0013$ for pithy stems). Indeed, this species nested more in the holes of *Acer* sp. logs and in the *Catalpa* sp. pithy stems than in those of any other log or stem species (Fig. 5a, b).

Discussion

We evaluated the colonization of human-made nesting structures by wild bees at 16 sites and over one or two consecutive years. There was no effect of the year of sampling or the year of installation of the soil squares on the

bee occurrence frequency or their abundance. In the bee hotels, the pattern of colonization of *Osmia bicornis* and the 'other species' were more affected by inter-annual fluctuations than by colonization history. The opposite was observed for *O. cornuta*. Soil texture did not influence the nesting of wild bees in the soil squares. Yet, in the hotels, *O. bicornis* nested more in *Acer* sp. logs or in *Catalpa* sp. stems than in any other log or stem species provided to them.

Use of human-made nesting structures in an urban environment

Over 2 years of sampling in the human-made nesting structures, we collected 37 soil-nesting bee species in the squares and 21 above-ground nesting species in the hotels, which represents 23 % of the 248 wild bee species recorded in the 16 urban and periurban sites in the area (Fortel 2014). Intensive sampling of bees usually leads to a low number of singletons because the numbers of bee specimens and that of singletons are negatively correlated (Williams et al. 2001). In the samples from bee hotels, we recorded only five species as singletons, i.e., 24 % of the species list, which is similar to the 19 % recorded in another study with the extensive sampling of the wild bee fauna in the area with pan trap and net captures ($\chi^2 = 0.064$, df $= 1$, $p = 0.799$; Fortel 2014). This suggests that the sampling of 1/8th of the nesting material for each type of nesting substrate plant species, at each site and for each year was an intensive strategy. For the soil squares, on the other hand, we sampled bees for only 45 min on a monthly basis, and we recorded 15 species as singletons, that is 40 % of the total number of species, which is different from the proportion of singletons in the overall sampling ($\chi^2 = 7.59$, df $= 1$, $p = 0.0059$) and indicates a much less intensive sampling effort. We recorded only six species of parasitic bees in the soil squares and two in the hotels, that is 15 % of the 46 parasitic species known in the area (Fortel 2014). Although the total of 58 species recorded in the human-made nesting structures is low compared to the regional richness of 248 species, we collected two species in the hotels that were not recorded using either pan-traps or insect net over the 2 years of sampling (one specimen of *Osmia tricornis* Latreille and 16 of *Megachile sculpturalis* Smith). *Osmia tricornis* is a solitary megachilid species from the mediterranean region (Leclercq 2001), and its presence confirms the Mediterranean influence in the area. *Megachile sculpturalis*, also known as the 'giant resin bee', is an exotic species introduced from central Asia that nests in pre-existing holes in logs or stems and was first recorded in France nearby Marseille along the Mediterranean shore in 2008 (Vereecken and Barbier 2009). Interestingly, this species also arrived in the United States in 1997 and has since spread quickly over a wide area (Mangum and Sumner 2003). It is now considered to be an invasive species in North America,
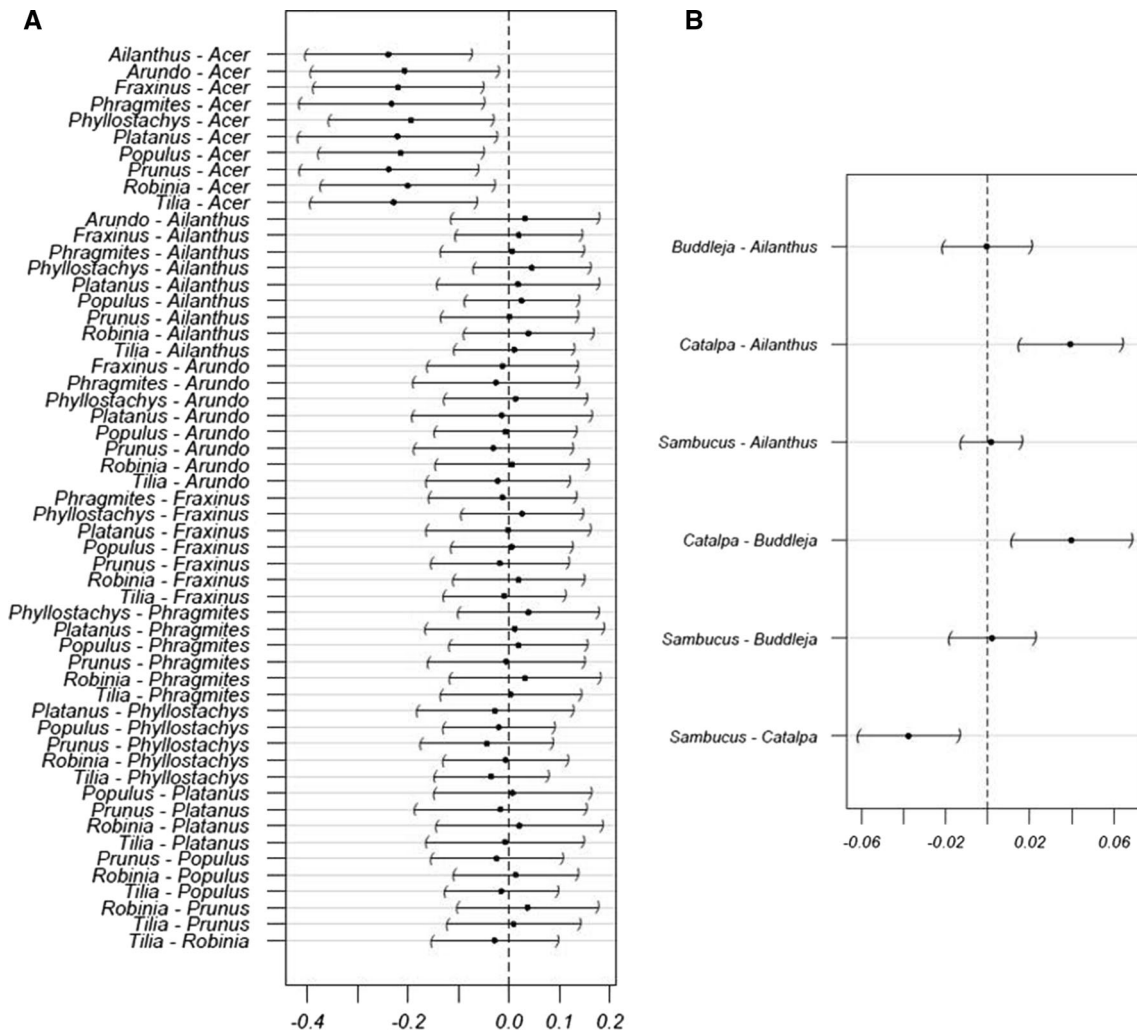
Fig. 5 Pairwise comparisons of the emergence rate of *Osmia bicornis* among holes in species of logs and hollow stems (**a**) and among species of pithy stems (**b**). There is a significant difference in preference between species if the 95 % confidence interval of the difference in means (*horizontal line*) does not include the null value

with aggressive behavior towards some local bee species using similar nesting resources (Laport and Minckley 2012; Roulston and Malfi 2012). The 16 specimens recorded here were all collected from bee hotels in the park of Gerland in Lyon, which is located along the Rhône river. *Megachile sculpturalis* has a generalist pollen diet in France like in the USA (Mangum and Sumner 2003; Vereecken and Barbier 2009) and its occurrence in Lyon suggests that it is also invasive in France. Thus, bee hotels can provide a useful tool to promote but also monitor the populations of above-ground nesting bees.

Nesting fidelity

Bees spend a lot of time and energy searching for suitable nesting sites, so any behavior that makes this process more efficient should be selected for (Brockmann 1980;

McCorquodale 1989; Potts and Willmer 1997). Females that emerged the previous season may learn the position and patch quality of their natal nest and return to that area (Potts and Willmer 1997). In the hotels, the occupation rate of *O. bicornis* was lower in 2013 than in 2012, but we collected as many specimens of *O. bicornis* in 2012 and in 2013. This means that *O. bicornis* was less frequent in 2013 than in 2012 samples, but it was as abundant. *Osmia bicornis* has a gregarious nesting behavior (Torchio et al. 1987; Krunić et al. 1995), and is philopatric (Neumann and Seidelmann 2006), i.e., the offspring prefer to nest in proximity to the parental nest (Shields 1982). Philopatry is probably an important factor in maintaining spatial stability of the nest aggregations of gregarious species in subsequent years (Polidori et al. 2006). Also, the presence of other individuals, or their nests, may provide a visual stimulus for further nesting at a given site by social facilitation

(Rubink 1978). For solitary bees which nest gregariously, the nest recognition appears to be dictated by involving both visual and olfactory cues (Anzenberger 1986; Raw 1992; Guedot et al. 2006). For example, Pitts-Singer (2007) tested the attraction of three species, *Osmia lignaria* Say, *Megachile rotundata* (Fabricius), and *M. pugnata* Say, to various components associated with their old nest cavities, or chemical extracts of these components. Female bees of these species are known to nest in or near old nest cavities, implying that remnant nest components are important cues for bees looking for nest cavities. She showed that female bees were attracted to components that may provide species-specific cues or indicate conspecific nesting activity (Pitts-Singer 2007). However, the use of odor cues from old nests for nest establishment should not be confused with the phenomenon of how these bees also will also build nests next to conspecifics once a few nests are initiated in a nesting board (Pitts-Singer 2007). In some cases, philopatry is associated with gregariousness (Michener et al. 1958), but, in this study, the population of *other species* had the same pattern of change as that of *O. bicornis*. For *O. cornuta*, the age of bee hotel nesting materials had an effect on the colonization, with 2-year old nesting structures being more colonized than 1-year old ones. The species other than *O. bicornis* and *O. cornuta* were less frequent, but as abundant in the hotels built in the winter of 2010/2011 in the samples that emerged in 2013 than in those of 2012. The colonization of these species was more affected by interannual variations than by the age of the nesting structure. Another factor that could explain the observed tendencies is parasitism, which we did not study, although we captured several parasitic bee and non-bee species. Bee hotels facilitate the increase of parasites and predators caused by the unnaturally high nest densities and the fact that nesting site entrances are set up in two-dimensions rather than in the more three dimensional arrangement found in nature (e.g. erect plant stems, decaying logs; Wcislo 1996; MacIvor and Packer 2015). Encouraging different bee species to co-aggregate in a bee hotel might increase opportunity for parasites to attack related species (Macivor and Salehi 2014).

Although the four most abundant species in the soil squares were almost all non-solitary (Danforth et al. 2003; Oertli et al. 2005), no clear pattern of change was observed either in the occurrence or in the abundance in the diachronic and synchronic analyses. This may be a result of the low sampling intensity used to collect bees in the soil squares.

Substrate selection

In our study, the texture of soil had no influence on bee species richness. This result is not fully in agreement with those of Cane (1991) who concluded that bee species could

be separated in two groups depending on their soil preference. One group nested preferentially in sands, loamy sands and more rarely in sandy loams, while the other group nested mainly in loams (sandy-, silt-, sandy clay- or clay-; Cane 1991). Also, larger species tended to nest in soils with greater clay content (Cane 1991). It is also noteworthy that, for lack of time and because we could not find any reference indicating that bees might actually nest in our soil squares, there are several characteristics that we did not take into account in our study such as the availability of bare soil in the landscape, the level of compaction of the soil in our squares (hardness), and its slope and orientation in regards to sunshine, both of which are also important for nest site selection of ground-nesting bees (Wuellner 1999; Potts et al. 2005).

In the hotels, *O. bicornis* and *O. cornuta* nested in all of the available substrates. These two species show great flexibility in the nesting substrates that they use, especially *O. bicornis* (Coudrain et al. 2015). Furthermore, *O. bicornis* was the only bee species that displayed nesting substrate preferences (for stems of *Catalpa* sp. and logs of *Acer sp.*). *Catalpa* sp. is a species with pithy stems, so bees have to dig their own cavities to use them.

Management implications and conclusions

That a diverse wild bee fauna (i.e., 57 species, which is 19.5 % of the total number of species found in this area (Fortel et al. 2014)) used our artificial nesting structures is an important result that highlights the usefulness of these structures to manage urban areas to encourage wild bees. Yet, as we discussed, it further studies would be needed to monitor the changes in colonization and bee community structure over more than 2 years to evaluate the evolution of parasitism in the nesting structures. Much attention in the past has focused upon improving floral resources available for bees and conserving and enhancing floral communities (Potts et al. 2003; Mader et al. 2011; Kirk and Howes 2012). However, to date little effort has focused upon the complementary and critical need for nesting resource provisioning. Proper urban management requires both resources to be available to attract and sustain diverse bee communities and the pollination services they provide. Furthermore, in addition to the direct usefulness of human-made nesting sites for bees, those structures are also a powerful tool to raise the awareness of urban citizens about biodiversity and ecosystem services.

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