Acta Oecologica 105 (2020) 103559

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Plant-pollinator interactions on green roofs are mediated by substrate characteristics and plant community composition

Yann Dusza[a,*], Yvan Kraepiel[a], Luc Abbadie[a], Sébastien Barot[a], David Carmignac[a], Isabelle Dajoz[a], Emmanuel Gendreau[a], Jean-Christophe Lata[a,b], Jacques Meriguet[c], Eric Motard[a], Xavier Raynaud[a]

[a] Sorbonne Université, CNRS, IRD, INRAE, Université de Paris , UPEC, Institute of Ecology and Environmental Sciences–Paris (IEES-Paris), 4 Place Jussieu, 75005, Paris, France

[b] Department of Geoecology and Geochemistry, Institute of Natural Resources, Tomsk Polytechnic University, Lenin Avenue, 30, 634050, Tomsk, Russia

[c] Institut de Biologie de l'Ecole Normale Supérieure, CNRS, INSERM, PSL Research University, 46 rue d'Ulm, 75005, Paris, France

ARTICLE INFO

Keywords:
Urban ecology
Soil-plant interactions
Pollination
Substrate depth and type
Plant community
Biodiversity

ABSTRACT

Green roofs can support pollinator communities in cities. However, little is known about the influence of green roof characteristics such as substrate and vegetation type on the abundance and diversity of attracted pollinators. Here we aimed to assess how green roof design impacts their attractiveness to pollinators. Using mesocosms on a rooftop in Paris (France), we studied the impact of two substrate types, two substrate depths (10 and 30 cm) and either monocultures or mixtures of 5 plant species on plant pollinator interactions. In the case of mixtures, we also tested the effect of substrate type (natural soil *vs.* artificial substrate). We counted the number of floral units and recorded the visits by pollinators once a week from mid-June to mid-August. The pollinator assemblage visiting plant communities included 4 functional groups of pollinators: domesticated honey bees, bumble bees, solitary bees and syrphid flies. Effects of treatments on pollinator community composition were variable and plant species dependent. Deep monoculture treatments resulted in the highest number of floral units and visits. Although plants grown on natural soil had less floral units than on artificial substrate, both treatments resulted in a similar number of visits. This paper provides evidence that plant-pollinator interactions on green roofs are modulated by substrate type, substrate depth and plant community. We suggest that combining plant species with diverse flowering morphologies and phenologies can enhance pollinator diversity. When possible, increasing substrate depth can result in higher levels of attractiveness.

1. Introduction

Urbanisation is a major cause of the global pollinator decline because it is associated with habitat destruction and fragmentation (Steffan-Dewenter et al., 2002; McKinney, 2008; Potts et al., 2010). There is evidence that urbanisation reduces the functional diversity of pollinator species assemblages, with a shift from small specialist to large generalist species such as honey or bumble bees that can cover long horizontal and vertical distances to forage from patches to patches (Banaszak-Cibicka and Zmihorski, 2012; Braaker et al., 2013; Geslin et al., 2013; MacIvor et al., 2015; Deguines et al., 2016). In densely constructed environments characterized by resource scarcity for pollinators, the promotion of green areas and infrastructures with abundant and diverse floral resources can enhance pollinator diversity and abundance (McKinney, 2006; Banaszak-Cibicka and Zmihorski, 2012; Matteson et al., 2012; Geslin et al., 2016). Green roofs, as urban green infrastructures, can participate to support pollinator communities in addition to providing ecosystem services such as regulation of water runoff quantity and quality, urban heat island mitigation, air quality improvement, sound proofing or thermal protection of buildings (Oberndorfer et al., 2007; Lata et al., 2017). Designing green roofs to improve their attractiveness to pollinators has two purposes: supporting the pollination of the green roof plants and supporting diverse and abundant pollinator communities at the urban area scale, which should

* Corresponding author. Vertige International 4, rue René Martrenchar, Cenon, France.
E-mail addresses: y.dusza@gmail.com (Y. Dusza), yvan.kraepiel@sorbonne-universite.fr (Y. Kraepiel), luc.abbadie@sorbonne-universite.fr (L. Abbadie), sebastien.barot@ird.fr (S. Barot), david.carmignac@sorbonne-universite.fr (D. Carmignac), isabelle.dajoz@univ-paris-diderot.fr (I. Dajoz), emmanuel.gendreau@sorbonne-universite.fr (E. Gendreau), jean-christophe.lata@sorbonne-universite.fr (J.-C. Lata), meriguet@biologie.ens.fr (J. Meriguet), eric.motard@sorbonne-universite.fr (E. Motard), xavier.raynaud@sorbonne-universite.fr (X. Raynaud).

https://doi.org/10.1016/j.actao.2020.103559
Received 18 May 2019; Received in revised form 24 October 2019; Accepted 20 March 2020

subsequently help the maintenance of diverse plant communities in cities. Indeed, more than 80% of flowering species are insect-pollinated (Ollerton et al., 2012) and pollinator diversity plays a key role in the persistence of diverse plant communities (Fontaine et al., 2006). Overall, this should help promoting biodiversity at the whole city scale. Few studies have directly addressed green roof attractiveness to pollinators. Inventories have stressed the presence of diverse arthropod groups, including groups with pollinator species such as the Hymenoptera (Apidae), Lepidoptera, Diptera (Syrphidae) and Coleoptera (Brenneisen, 2006; Kadas, 2006; Macivor and Lundholm, 2011; Madre et al., 2013). Colla, Willis & Packer (2009) showed that the diversity of bees on a green roof in Toronto (Ontario, Canada) was not different from the diversity at ground level. On the contrary, Tonietto et al. (2011) and Ksiazek et al. (2012) found that native bees in Chicago (Illinois, United States) were present on green roofs but at lower abundance and diversity than in other urban habitats. Braaker et al. (2013) investigated the role of landscape configuration and spatial patterns (habitat connectivity) on arthropod communities among 40 green roofs and 40 ground sites in Zurich (Switzerland). They suggested that improving green roof design (vegetation and soil type) should increase the effectiveness of short-range pollinating species in cities.

Green roof substrates are designed to be light. They are usually based on materials such as pozzolan (a porous volcanic stone) or expanded clay (Ondoño et al., 2014). “Extensive” green roofs are based on substrates usually shallower than 15 cm and on low plant species diversity. Extensive green roofs theoretically require little maintenance. On the contrary, intensive green roofs have substrates deeper than 15 cm, can support more plant species but need more maintenance. Overall, extensive green roofs planted with the drought resistant *Sedum* species are the most widespread systems around the world (Vijayaraghavan, 2016). However, there is increasing evidence that most green roof ecosystem services depend on substrate type, substrate depth and plant community (Dusza et al., 2017). Testing different plant communities as well as substrates with different characteristics and depths should be important on the long run for green roofs. Many studies have provided guidelines to improve multiple ecosystem services through the choice of plant community and substrate composition (Lundholm, 2015; Vijayaraghavan, 2016; Dusza et al., 2017). But few authors have investigated the influence of plant community and substrate on pollinator communities (Hoffmann and Renner, 2017). Given the short bloom time of some *Sedum* species commonly used on green roofs, MacIvor et al. (2015) suggested that designers should be encouraged to plant green roofs with multiple species to provide food to pollinators over a longer period. Tonietto et al. (2011) showed that bee diversity on green roofs increased with the diversity of blooming plants. Overall, increasing plant diversity leads to the creation of more niches for organisms feeding on these plants, thereby promoting arthropod and pollinator diversity (Braaker et al., 2013; Madre et al., 2013, 2014). The role of substrate composition and depth on green roof attractiveness to pollinators has been less investigated, although there is evidence that substrate characteristics are strongly involved in plant development (Chenot et al., 2017). Higher plant biomass was found for higher nutrient contents in substrates (Rowe et al., 2012; Clark and Zheng, 2014; Kanechi et al., 2014) and deeper substrates (Durhman et al., 2007; Dunnett et al., 2008; Lu et al., 2015). Substrates with high porosities lead to higher plant development, as they present good aeration conditions for roots (Ondoño et al., 2015). Substrate composition and depth also affect various plant characteristics and functions such as leaf C/N ratio, stomatal density or transpiration (Dusza et al., 2017). Likewise, substrate composition and depth may affect, through changes in nutrient availability, plant traits related to pollination. Indeed, studies not focusing on green roofs suggested that soil characteristics and the availability of soil resources impact flower characteristics, which subsequently impact pollinators (Baude et al., 2011). Burkle and Irwin (2010) showed that adding nitrogen could lead to additional flowers production. Gorden and Adler (2013) observed that using fertilisers increased the volume of nectar and enhanced floral attractiveness. However, to our knowledge, the effect of substrate depth and type on green roof attractiveness to pollinators has been assessed only once (Kratschmer et al., 2018). This study examines the influence of plant community composition, substrate type and substrate depth on the abundance and diversity of visiting insect pollinators. We addressed this issue with a mesocosm experiment on a roof top in Paris (Ile-de-France, France). In Paris and its region, guidelines created by the city of Paris and the Ile de France Agency for Biodiversity specify that new green roofs should have a minimum substrate depth of 10 cm (Ville de Paris, 2012; Natureparif, 2013). The guidelines also highlight the need to test deeper substrates, as well as local and more natural substrates. Focusing on this context, we tested two substrate depths (10 vs. 30 cm), two substrate types (commercial substrate and natural, local soil), and five plant species grown either in monoculture or in mixture. We focused on the following questions: 1. Are abundance and functional diversity of pollinators affected by substrate depth and substrate type? 2. Are abundance and functional diversity of pollinators modified when plants are grown in mixture?

2. Material and methods

2.1. Experimental site and mesocosms

The experimental site (48°54′06N, 2°22′23E) was located in the city of Paris (Ile-de-France, France) under subatlantic climate. The study took place on a roof 30 m above ground level and was part of a bigger experiment aimed at studying the provision of ecological service by green roofs. The roof was surrounded by two buildings 6 m taller on its West and East sides. We installed 56 mesocosms (0.8×0.8 m^2) made of wooden trays lined on the inside with a waterproof membrane. Half of the mesocosms was 12 cm high, while the other half was 32 cm high. The bottom of each mesocosm was covered with a drainage layer consisting of a geotextile membrane with a 1 cm diameter perforated pipe (Teradrain FD200T1, Terrageos, Veurey Voroize, France) crossing the tray in the middle. A hole was drilled in the lowest part of the tray to connect the drainage pipe with a waterproof silicone tube to allow for drainage. A slight slope was set up (1.2%) to favour water flows out of the mesocosms.

2.2. Substrate material

Two different substrate types were used. The first was a substrate commercialised for green roofs, based on pozzolan (porous volcanic rock) and peat (i.D. Flore SP, Le Prieuré – Vegetal i.D., Moisy, France), hereafter named “artificial substrate”. The second was a natural sandy loam soil taken from a temperate grassland site (CEREEP-Ecotron Ile-de-France, Saint Pierre-lès-Nemours, France), hereafter named “natural soil”. The City of Paris and the Ile-de-France Agency for Biodiversity promote the use of local and natural soils for new green roofs. The natural soil was chosen to fulfil these requirements (Ville de Paris, 2012; Natureparif, 2013). Roots, plant debris and stones were removed from the natural soil by sieving (< 5 mm) before homogenization. Substrate characteristics are summarized in Table 1.

Table 1
Substrates characteristics (mean ± SE).

Soil characteristics	Natural soil	Artificial substrate
Type	Sandy-loam	Pozzolan-peat
Dry bulk density (kg.m^{-3})	1.6 ± 0.01	1.1 ± 0.02
Saturated bulk density (kg.m^{-3})	2.1 ± 0,03	1.5 ± 0.03
Water retention (% of dry soil)	33 ± 2.13	41 ± 2.99
C content (g.kg^{-1})	9.71 ± 0.26	51.14 ± 0.39
N content (g.kg^{-1})	0.74 ± 0.03	4.97 ± 0.04
pH	7.7 ± 0.09	7.4 ± 0.18

2.3. Plant material

Mesocosms were planted with monocultures or 5 species mixtures of *Centaurea jacea*, *Dianthus carthusianorum*, *Hylotelephium maximum, Lotus corniculatus* and *Koeleria pyramidata*.

Centaurea jacea (Asteraceae) is a perennial species, with large, purple, tubular flowers grouped in capitulae. It is mainly pollinated by large bees and hoverflies, and to a lesser extent by butterflies (Albrecht et al., 2009). Flowering period ranges from June to September.

Dianthus carthusianorum (Caryophyllaceae) is a perennial species, with large, purple, open flowers grouped by 2–8. It is mainly pollinated by butterflies (Bloch et al., 2006) and flowers from June to September.

Hylotelephium maximum (Crassulaceae) is a perennial species with small, white, open flowers grouped in large corymbs. It is pollinated by bees and butterflies and flowers in August and September.

Lotus corniculatus (Fabaceae) is a perennial, nitrogen fixating species, with small, yellow tubular flowers. It is mainly pollinated by *Bombus* species (Pellissier et al., 2012) and flowers from May to September.

Koeleria pyramidata (Poaceae) is a perennial wind pollinated grass species that produce leaves during the whole growing season.

Plant species were chosen on the basis that they were native to the Ile-de-France region (France), were known to have already been used on green roofs and were tested, among other plant species, for their ability to survive under dry conditions while providing high levels of water retention and runoff quality as well as air cooling (Dusza et al., 2017). This resulted in the inclusion of the grass *K. pyramidata*, although this species is not insect-pollinated. Previous studies have shown that the main pollinators of *L. corniculatus* are bumble bees. For all other plant species, pollinating insects also include other bees and pollinators of *D. carthusianorum* also include butterflies (Arnold et al., 2010; Lundgren et al., 2015). Seed germination was carried out under greenhouse conditions (University Pierre et Marie Curie, Paris, France) and seedlings of at least 5 cm tall were planted in mesocosms on July 4th, 2014. 25 plants were planted in each mesocosm on a regular grid spaced by 13.5 cm. During the first two months, mesocosms were watered once a week (10 L per mesocosm) to ensure optimal growth conditions and no plant mortality was observed during the start of the experiment. Contrary to artificial substrates, plant colonization was observed in natural treatments. Plants different from the selected species were regularly weeded out.

2.4. Experimental design

The experimental design is shown in Fig. 1 and was aimed at testing the effects of substrate type, substrate depth and plant diversity on pollinator communities visiting green roofs. Artificial substrate mesocosms were planted with either a monoculture of one of the five species (25 plants), or a mixture of the five species (25 plants, 5 individuals per plant species). Natural soil mesocosms were only planted with the 5 species mixture. For each substrate type, mesocosms were filled with either 10 cm or 30 cm of substrate, hereafter named “shallow” or “deep” treatments, respectively. 10 cm corresponds to the minimum depth required by the City of Paris and the Ile-de-France Agency for Biodiversity for the implementation of new green roofs (Ville de Paris, 2012; Natureparif, 2013). The deep treatment corresponds to the will of these institutions to develop green roofs based on deeper and more natural soils. Each combination of treatments was replicated 4 times, making a total of 8 natural soil mesocosms (2 depths, mixture only) and 48 artificial mesocosms (2 depths, 6 vegetation types: 5 monocultures + 1 mixture). In mixtures, individuals of each species were assigned a randomly chosen position within the mesocosm.

Because higher buildings around the roof could lead to heterogeneity in climatic parameters, the roof was divided into four blocks, each containing one replicate of all experimental treatments. Each block was equipped with a weather station (Vantage pro II, Cima technologie, Montanay, France). No difference between blocks was detected in the daily amount of light, rain and temperatures during the experiment (July 2014 to September 2015). Monthly air temperature during the study period were 19.3 °C (June), 21.6 °C (July) and 21.9 °C (August). During the pollination experiment, mesocosms received 57 mm water from natural rain. Each mesocosm was watered with 5 L of water to limit water stress when rain did not occur for 7 consecutive days.

2.5. Plant-pollinator observations

Plant-pollinator interactions were recorded as long as at least two species were flowering simultaneously. This resulted in a two months measurement period, from June 10th to August 12th 2015. This period encompassed the flowering peaks of all species: the earliest species (*D. carthusianorum*) had its flowering peak during the second half of June, while the latest species (*H. maximum*) had its flowering peak at the beginning of August. An observation round was carried out about once a week. Observations were only carried out on sunny days, between 10 a.m. and 5 p.m., avoiding windy days. During an observation round, all visits by flower–visiting insects foraging on the experimental plant communities were recorded for 5 min on each mesocosm. Because we expected interactive effects between substrate treatments (depth and type) and plant species identity, pollinator visits were recorded at the

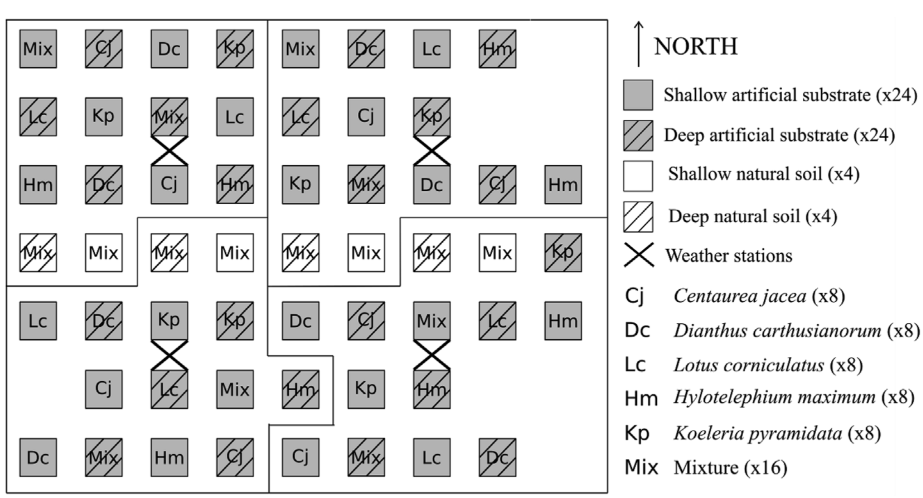

Fig. 1. Schematic representation of the experimental design.

Table 2
Anova/Ancova tables for artificial substrate treatments. **(a)** Number of floral units and visits per mesocosm as a function of depth and vegetation type. **(b)** Number of visits per plant for each plant species as a function of the number of floral units, vegetation type and substrate depth. Missing factors or values correspond to factors and interactions removed from the complete models after the simplifications using the Akaike Information Criterion. “R^2”stands for the squared R of the fitted model. “FL” stands for the number of floral units and “Veg” for Vegetation type.

a

Plant	Model		ANOVA df/F value/p-value			
	R^2	p-value		Depth	Veg	Depth*Veg
Number of floral units	0.87	1.48 10^{-5}	DF	1	1	1
			F value	14.82	49.24	14.62
			p-value	0.002	1.4 10^{-5}	0.002
Number of visits	0.91	2.01 10^{-6}	DF	1	1	1
			F value	28.67	71.68	14.54
			p-value	1.72 10^{-4}	2.10 10^{-6}	0.002

b

Plant species	Model		ANCOVA df/F value/p-value			
	R^2	p-value		FL	Veg	FL* Depth
Centaurea jacea	0.22	4.90 10^{-7}	DF	1	1	1
			F-value	18.01	5.13	13.09
			p-value	4.11 10^{-5}	0.025	4.22 10^{-4}
Dianthus carthusianorum	0.31	5.51 10^{-10}	DF	1		
			F-value	46.66		
			p-value	5.51 10^{-10}		
Hylotelephium maximum	0.61	9.97 10^{-7}	DF	1	1	
			F-value	28.88	17.33	
			p-value	8.98 10^{-6}	2.56 10^{-4}	
Lotus corniculatus	0.36	4.91 10^{-13}	DF	1		
			F-value	66.188		
			p-value	4.91 10^{-13}		

plant level in all mesocosms. The order of observed mesocosms was modified at each round to limit the risk of a “time of day” effect. Before each observation round, the abundances of flowers in each mesocosm were evaluated: we counted open flowers of all species, with the exception of *C. jacea* for which we counted the number of capitulae. Hereafter, we refer to flowers and capitulae as “floral units”. To assess pollinator abundance and diversity, we used a non destructive method based on pollinator morphotypes (Geslin et al., 2013; Aguirre-gutiérrez, Kissling and Carvalheiro, 2016; Desaegher et al., 2017). Three groups were distinguished within the Apidae superfamily. 1. Bumble bees (species from the *Bombus* genus) 2. Solitary bees (group enclosing all Apidae species, except the *Bombus* genus and domesticated honey bees. 3. Domesticated honey bees (*Apis melifera*). The 3 other groups were 4. Syrphidae 5. Lepidopterae 6. Coleopterae.

2.6. Statistical analyses

Data analyses were performed using the R statistical software (version 3.2.2; R Core Team, 2015). Because the number of visits in a given mesocosm could also depend on the characteristics of neighbouring mesocosms, we checked for potential spatial autocorrelation among mesocosms. We computed a distance matrix for the total number of visits within each mesocosm and a distance matrix for the spatial distance between mesocosms. We tested the correlation between the two matrices, i.e. the spatial autocorrelation, with a Mantel test (9999 permutations, *ncf* package; Bjornstad, 2016). Since there was no spatial autocorrelation ($p = 0.56$), the number of visits in neighbouring mesocosms was considered independent and we used standard linear models without autocorrelation term.

The “number of visits per mesocosm” was defined for each mesocosm as the total number of visits over the course of the experiment. In order to compare vegetation types (mixtures vs. monocultures), the 5 plant species grown in monocultures were considered together to calculate the mean number of visits per mesocosm for monocultures within each replicate block. For each species inside a mesocosm, the “number of visits per plant” was defined as the number of visits received by an individual plant. It was obtained by dividing the total number of visits on a species by the number of plant individuals for this species inside the mesocosm (25 for monoculture, 5 for mixtures). Although *K. pyramidata* is a wind-pollinated species, it was kept for analyses because its presence in mixtures might affect other plant-pollinator interactions through mechanisms such as competition for belowground resources (Flacher et al., 2015). The same approach was applied to calculate the “number of floral units per mesocosm” and the “number of floral units per plant”. As the data for the “number of floral units per mesocosm” and the “number of visits per flower” are averages, and not real count data, we fitted standard linear models. In any case, we checked for the normality and homoscedasticity of the residuals which justifies the use of standard linear models and data were log transformed when the residuals were non-normal.

Due to the unbalanced design, analyses were performed first within the artificial substrate treatment to test for the effects of vegetation type (types of monocultures and mixtures) and substrate depth and, second, within the mixture treatment to test for the effects of substrate type and depth. To evaluate whether the number of visits per mesocosm and the number of floral units differed between the mixture and the

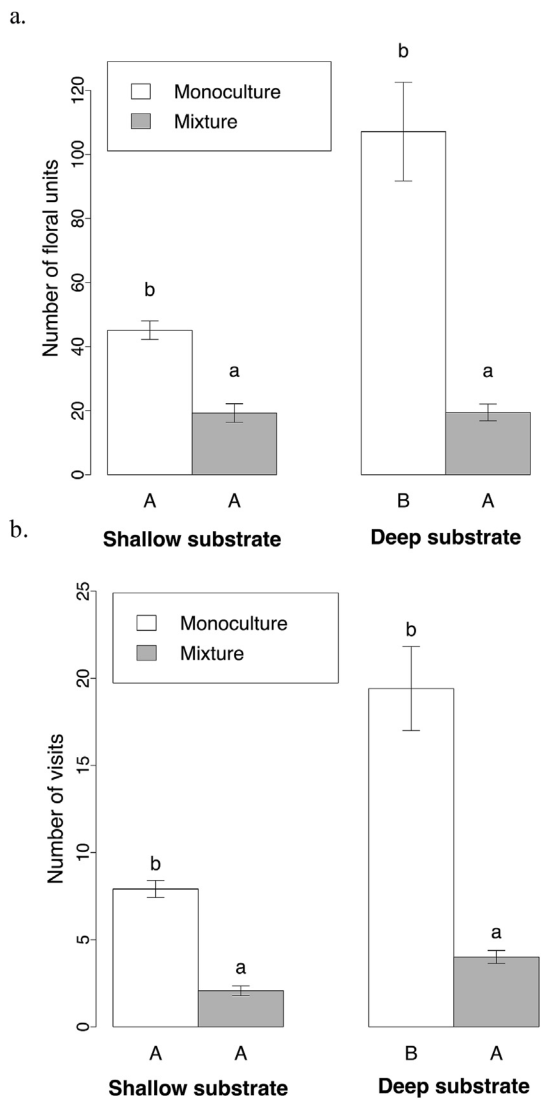

Fig. 2. Average number of floral units (a) and visits (b) per mesocosm as a function of vegetation type and substrate depth for artificial substrate treatments (± SE). Lower case letters indicate differences ($p < 0.05$) between vegetation types within each substrate depth. Capital letters indicate differences ($p < 0.05$) between substrate depth within each vegetation type.

monoculture treatments, simple linear models were fitted with substrate depth and vegetation type as factors. Pairwise comparisons were calculated from these different models using the Tukey-Kramer method (*lsmeans* package; Lenth, 2015). We used an analysis of covariance (ANCOVA) to test whether the number of visits per plant for each plant species was influenced by the number of floral units per plant and whether these relationships differed among growing conditions (vegetation type and substrate depth). For each plant species, a complete simple linear model including all factors and their interactions was simplified based on the Akaike Information Criterion. During the experiment, very few Lepidoptera, Coleoptera or Diptera other than Syrphidae visited the mesocosms and were merged into a single category "Other". This category represents less than 5% of the total visits. To test whether the proportion of visits by a given pollinator group on a given plant species differed between combinations of vegetation type (mixture vs. monoculture) and substrate depth, we proceeded in two steps. First, for each plant species, we fitted a multinomial model to the proportion of visits of all flower visitor groups. Then, if the treatment had a significant effect on these proportions of visits, for each combination of plant species and flower visitor groups, a second binomial model was fitted for each pollinator group (Galyean and Wester, 2010) to test for the effect of treatments on the proportion of visits by group on each plant species. The same type of analysis was performed to test for differences between combinations of substrate type and substrate depth in mesocosms with plant mixtures.

3. Results

3.1. *Effect of vegetation type and substrate depth in artificial substrate treatments*

3.1.1. *Phenology, number of floral units and visits per mesocosm*

Overall, treatments did not alter the timing of flowering. *D.Vertige International 4, rue René Martrenchar, Cenon, France. carthusianorum* had its flowering peak mid-june in all treatments, *L corniculatus* at the start of July, *C. jacea* at the start of August and *H. telephium* mid-August. However, treatments altered the number of floral units as well as the number of visits. The number of floral units per mesocosm was 2 times higher in shallow monoculture treatments than in shallow mixtures and 5 times higher in deep monoculture treatments than in deep mixtures (Table 2a, Fig. 2a). A depth effect was found only for monocultures, with about 2 times more floral units per mesocosm when plants were grown on deep substrate. The number of visits per mesocosm followed the same trend and was, on average, 3 times higher for plants grown in monocultures than for plants grown in mixture in the deep substrate treatments and 5 times higher in the shallow treatment (Table 2a, Fig. 2b). For monocultures, there were twice more visits per mesocosm when plants were grown on deep substrate.

3.1.2. *Visits per plant for each plant species*

For all plant species, the number of visits per plant increased with the number of floral units per plant (Table 2b, Fig. 3). For *D. carthusianorum* and *L. corniculatus*, the number of floral units was the only parameter influencing the number of visits (Fig. 3a and b.) For *H. maximum*, the number of visits increased with the number of floral units with the same slope for all treatments but the regression line for monocultures was above the one for mixtures: for the same number of floral units, monocultures always induced more visits (Fig. 3c). For *C. jacea* the number of visits increased with the number of flower units for all treatments and the slope of the relation was steeper for monocultures than for mixtures (Fig. 3d). For this species, we also found a substrate depth effect, with more visits per floral unit in the deep treatment. Within each vegetation type, the slope of the relation between visits and flower units was steeper for deep treatments than for shallow treatments. Overall, when depth or vegetation type affected the number of visits, monocultures and deep substrates were the most attractive treatments.

3.1.3. *Composition of pollinator communities*

Whatever the treatment, *C. jacea* was mostly visited by solitary bees, *D. carthusianorum* and *H. maximum* by honey bees (Fig. 4). *L. corniculatus* was mostly visited by bumble bees except when grown in monocultures and deep substrate where a shift towards solitary bees and honey bees as the dominant visiting group was observed (Fig. 4). Proportions of pollinators were affected by plant species, substrate depth, vegetation type and the substrate depth:vegetation type interaction (multinomial model, $P < 0.01$ in all cases; Fig. 4). In the case of *C. jacea*, the most balanced composition was found for mixtures on deep substrate, as solitary bees accounted for about 43%, honey bees for 34% and bumble bees for 23% of the total number of visits. In the three other treatments, solitary bees were more dominant, accounting for 52% (monoculture on shallow substrate) to 75% of the total number of visitors (mixture on shallow substrate). Monocultures of *D. carthusianorum*, either in deep or shallow substrate, were characterized by at least 75% of honey bees. By comparison, *D. carthusianorum* grown in mixtures (whatever the substrate depth) led to more balanced

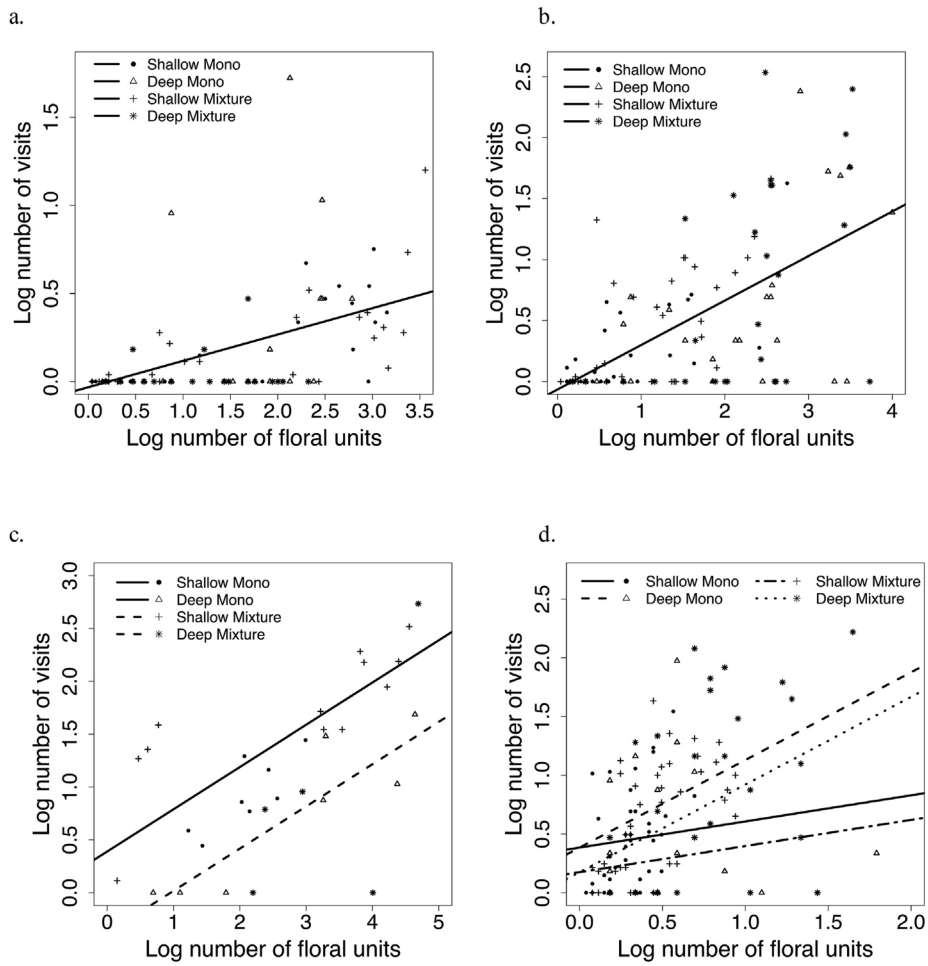

Fig.3. Number of visits per plant against the number of floral units for each plant species grown on artificial substrate as a function of vegetation type and substrate depth. a = *Dianthus carthusianorum*; **b** = *Lotus corniculatus*; **c** = *Hylotelephium maximum*; **d** = *Centaurea jacea*. Regressions lines are based on ANCOVA results. The different number of lines between plant species is due to the removal of factors that did not influence the relation between number of visits and number of floral units, based on the simplification of the complete ANCOVA model using the Akaike Information Criterion (Table 2b). "Mono" stands for "monoculture".

communities, with the proportion of honey bees reduced to about 40% and a higher presence of bumble bees and syrphid flies. For *H. maximum*, the less diverse visiting community was found in mixtures grown on deep substrate, as honey bees accounted for almost 91% of total pollinators. Both shallow treatments (mixture or monoculture) led to proportions of honey bees below 70%. The shallow mixture treatment presented the most balanced community, as bumble bees and solitary bees were almost equally represented (about 15%), while monocultures were almost uniquely visited by solitary and honey bees. For *L. corniculatus*, the most balanced community was found for the monoculture treatment planted on deep substrate, with proportions of 29, 30 and 37% of respectively bumble bees, honey bees and solitary bees. By comparison, bumble bees accounted for at least 60% of total pollinators for all other treatments. However, syrphid flies accounted for 22% of visitors in monocultures planted on shallow substrate, while this proportion was below 7% for all other treatments.

3.2. Effect of substrate type and depth in mixture treatments

Only mixtures were grown on both substrate types. Here we focus on the influence of substrate type and depth on pollinator abundance and pollinator community composition in mixtures.

3.2.1. Number of floral units and visits per mesocosm and per plant

While no depth effect was found on the number of floral units per mesocosm, there were 2 times more floral units in artificial substrate than in natural soil at each depth (Table 3a, Fig. 5a). However, neither substrate type nor depth had an effect on the number of visits per mesocosm for mixtures (Table 3a, Fig. 5b). The number of visits per plant for *D. carthusianorum* and *H. maximum* was independent on the number of floral units, substrate type and substrate depth (Table 3b). The number of visits per plant was positively linked to the number of floral units for *C. jacea* (Fig. 6a) and *L. corniculatus* (Fig. 6b). This relationship was affected by substrate type: the number of visits increased with the number of flowers units quicker for the natural soil than for the artificial substrate.

3.2.2. Composition of pollinator communities

Substrate type and depth had variable effects on pollinator communities according to plant species (Fig. 7). There was a significant effect of substrate type, depth and their interactions on the proportion of visits received by *H. maximum* and *L. corniculatus* ($P < 0.05$ at the most), an effect of the Type:Depth interaction on visits received by *C jacea* ($P < 0.01$) and no effect on visits received by *D carthusianorum* ($P > 0.3$). For *C. jacea*, the most balanced visiting community was found for the deep artificial substrate treatment that was the only treatment where solitary bees did not reach 50% of total visitors. Only honey bees were observed on *H. maximum* grown in shallow natural soil while on shallow artificial substrate, *H. maximum* received up to 15% visits by bumble bees and solitary bees. For *L. corniculatus*, distinct patterns were found for each substrate type. In the artificial substrate,

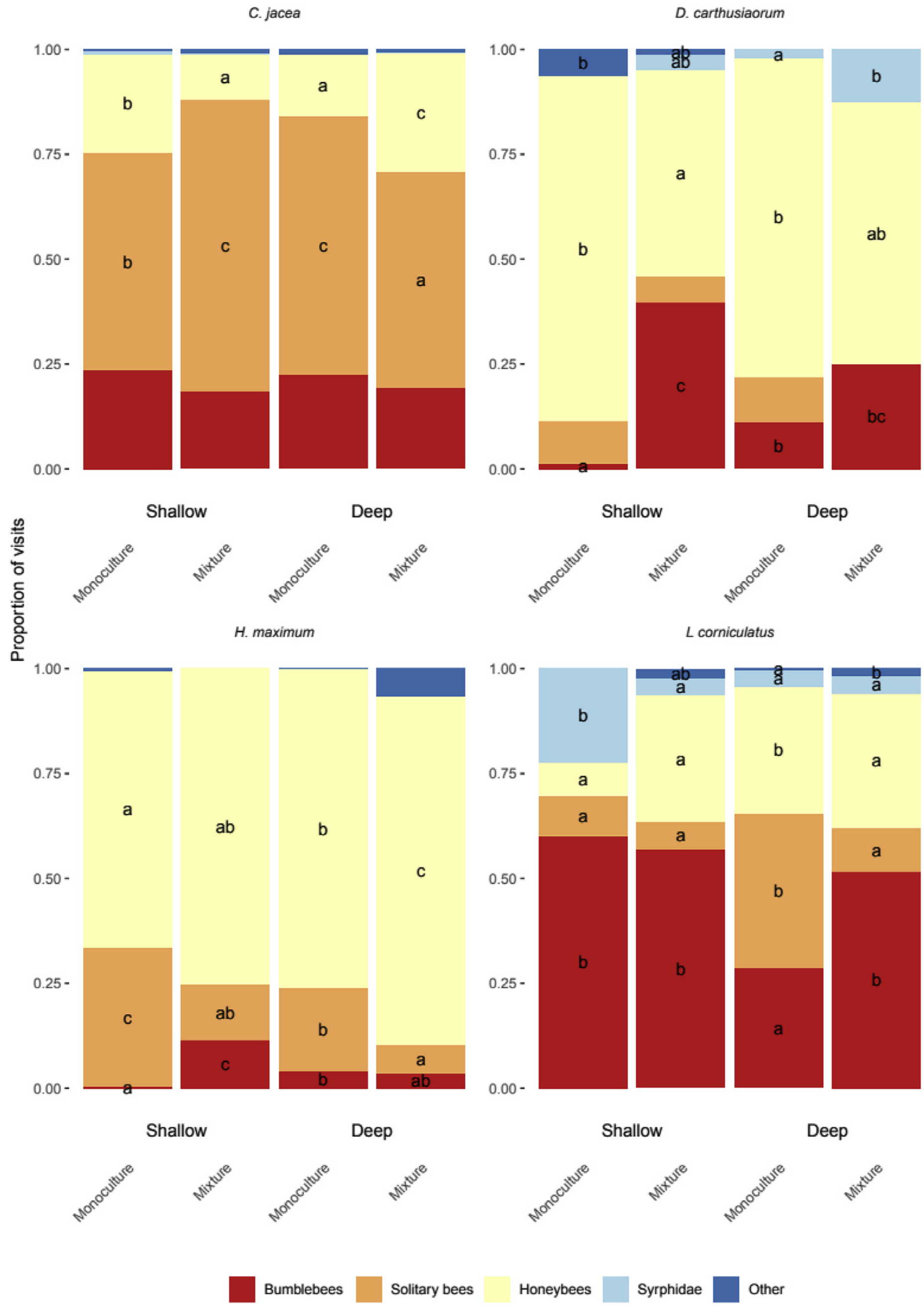

Fig. 4. Pollinator community composition for each plant species grown on artificial substrate as a function of vegetation type and substrate depth. Within each group of pollinators, letters indicate difference in proportions ($p < 0.05$) between treatments. Letters are only shown when there are differences between treatments.

bumble bees accounted for the majority of pollinators, while honey bees accounted for the majority of visitors in natural soil. Solitary bees and syrphid flies were more represented in the artificial substrate treatment, though differences were small.

4. Discussion

4.1. Functional diversity of pollinators

Given the short bloom time of *Sedum* species commonly used on green roofs, MacIvor et al. (2015) encouraged to plant green roofs with multiple species to provide resources for pollinators during a longer period of time. In our experiment, plants with diverse flower morphology and flowering phenologies were used, allowing the continuous presence of flowers and pollinators during at least two months. In particular, we have used species local to the Ile de France region so that these species should be well-adapted to climatic conditions (Van Mechelen et al., 2014) and their natural pollinators should be present. The choice of plant species had a strong role in determining the composition of the visiting community. *H. maximum* attracted almost exclusively honey bees while *C. jacea* was mostly visited by solitary bees and *L. corniculatus* attracted a high proportion of bumble bees. Overall, Syrphidae were rarely observed but neither Lepidoptera species nor Coleoptera species were found foraging during the two months observations. Apidae species are known to pollinate the selected plant species (Steffan-Dewenter et al., 2002; Arnold et al., 2010; Pellissier et al., 2012; Lundgren et al., 2015). However, pollinators of *D. carthusianorum* include a large proportion of Lepidoptera in natural

Table 3
Anova/Ancova tables for mixture treatments. **(a)** Number of floral units and visits per mesocosm as a function of substrate depth and substrate type. **(b)** Number of visits for each plant species as a function of the number of floral units, substrate type and substrate depth. Missing factors and values correspond to factors removed from the complete models after the simplification using the Akaike Information Criterion. "R^2" stands for the squared R of the fitted model. "FL" stands for the number of floral units, and "S" for substrate type. In table b, the model did not fit for *D. carthusianorum* and *H. maximum* ($p > 0.05$).

a.

Plant species	Model		ANOVA degrees of freedom/F-value/p-value			
	R^2	p-value		Depth	Substrate type	Depth*S
Number of floral units	0.65	0.004	DF	1	1	1
			F-value	0.290	21.869	0.193
			p-value	0.600	$5.36\ 10^{-4}$	0.667
Number of visits	0.37	0.022	DF	1	1	1
			F-value	2.810	1.203	1.133
			p-value	0.120	0.294	0.308

b

Plant species	Model		ANCOVA degrees of freedom/F-value/p-value			
	R^2	p-value		FL	Substrate type	FL*S
Centaurea jacea	0.37	$1.25\ 10^{-12}$	DF	1		1
			F value	2.56		66.23
			p-value	0.11		$3.36\ 10^{-13}$
Lotus corniculatus	0.30	$3.47\ 10^{-8}$	DF	1	1	1
			F value	18.86	25.07	7.69
			p-value	$3.00\ 10^{-5}$	$1.97\ 10^{-6}$	0.006

ecosystems (Bloch et al., 2006). The absence of Lepidoptera in our experiment might be linked to the overall decline of this group in cities (Bloch et al., 2006; Deguines et al., 2012), and more generally to biotic homogenization favouring generalist taxa, that does not include Lepidoptera or Coleoptera (Desguines et al., 2016). Our results are consistent with other studies reporting that urban areas are profitable to bees (Winfree et al., 2007; Carré et al., 2009; Fortel et al., 2014; Baldock et al., 2015) because of their ability to fly from patches to patches and forage on a large set of plant species (Biesmeijer et al., 2006; Geslin et al., 2013). Our results are also consistent with studies showing high bee abundance on green roofs (Colla et al., 2009; Tonietto et al., 2011; Ksiazek et al., 2012). Effects of treatments on pollinator community composition were variable, plant species dependent and weak, confirming that the plant identity was the most important factor affecting the functional diversity. Moreover, in mixtures, pollinator communities were more balanced compared to monocultures: as different plant species attract different pollinator communities, pollinator community that visits mixtures is more diverse but less variable than those visiting monocultures. The artificial substrate was also associated with more balanced communities than the natural soil. In particular, the syrphid flies were more abundant on *L. corniculatus* grown in the artificial substrate than in the natural soil. The same number of floral units per plant led to more visits for the natural soil than for the artificial substrate, suggesting that a reduced competition between pollinators might have allowed more frequent syrphid flies visits for the artificial substrate. Future research should address more precisely the influence of soil-plant interactions on pollinator diversity. For instance, soil-plant interactions affect below-ground competition for resources and consequently the floral display (Flacher et al., 2015). This can in turn alter the provision of habitat and resources for arthropods and pollinating insects so that the number of visits (Flacher et al., 2017) as well as the visiting community diversity can be altered by soil-plant interactions (Flacher et al., 2020).

4.2. Abundance of pollinators

As expected, at the plant level, the more floral units, the greater the number of visits the plant received.

Overall monocultures produced more flowers, which induced more plant-pollinator interactions than mixtures. Competition for resources among the different species in mixtures could have led to a decrease in floral units numbers (Flacher et al., 2015), since producing flowers is costly (Snow, 1989). Increasing substrate depth had an effect on the number of floral units and visits per mesocosm only when plants were grown in monocultures and not in mixtures. Using the same soil, depth and plant species as in our experiment, Dusza et al. (2017) showed that the species grown in monoculture had a higher biomass in deep artificial substrate due to a higher nutrient content. Likewise, in our experiment, increasing depth in monoculture led to more floral units probably because of the higher nutrient content. This is consistent with several studies showing that increasing depth induces a higher plant development on green roofs (Dunnett et al., 2008; Durhman et al., 2007; Lu et al., 2015; Thuring et al., 2010). In mixtures, interspecific interactions could have prevented the benefits of increasing substrate depth due to a lower investment in reproductive parts as suggested by Flacher et al. (2015). Besides, it has been shown that green roof substrate nitrogen availability lead to higher biomass on green roofs (Rowe et al., 2012; Clark and Zheng, 2014; Kanechi et al., 2014). Studies in natural ecosystems have also shown that soils with more nitrogen could lead to more abundant flowers (Burkle and Irwin, 2010). Likewise, the higher nitrogen availability in the artificial substrate probably explains the presence of more floral units per mesocosm as compared to the natural soil.

However, for the same number of floral units per plant, the number of visits per plant was higher for the natural soil than for the artificial substrate. Similarly, when we found depth effects, the same number of floral units for a plant grown in the deep substrate induced more visits than the shallow substrate. This suggests that the number of floral units is not the only characteristic that influences attractiveness when dealing with different soil compositions and depths. In particular, soil

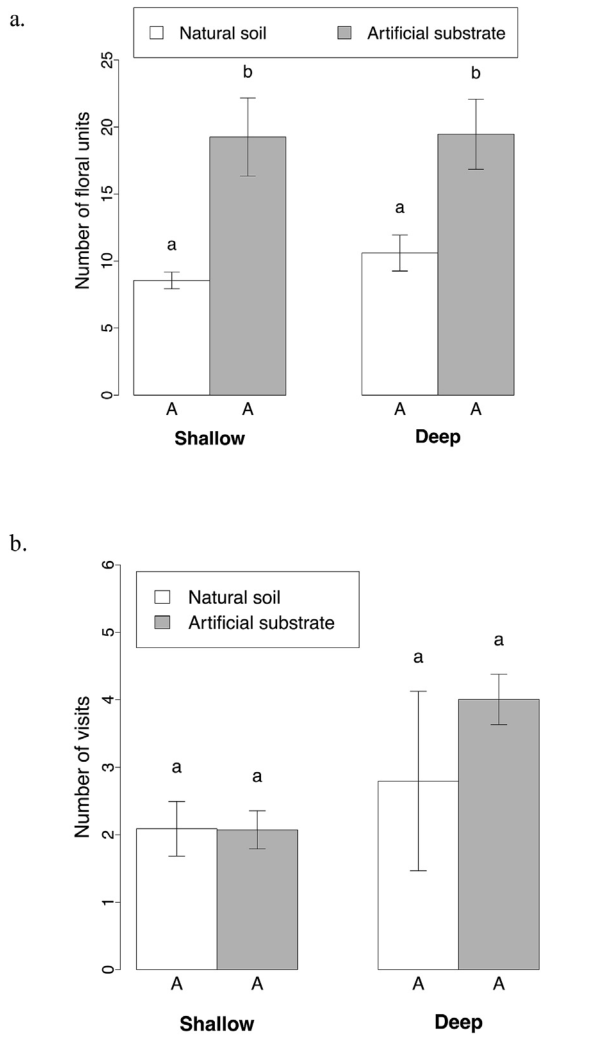

Fig. 5. Average number of floral units (a) and visits (b) as a function of substrate depth and substrate type for mixture treatments (± SE). Lower case letters indicate differences ($p < 0.05$) between substrate type within each substrate depth. Capital letters indicate differences ($p < 0.05$) between substrate depths within each substrate type.

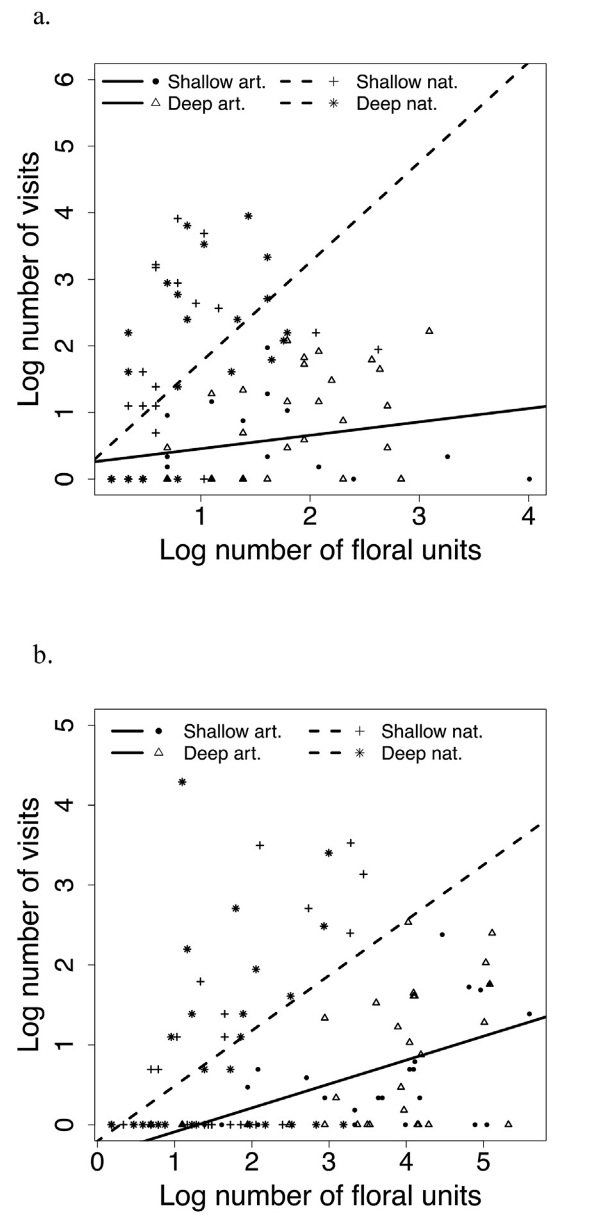

Fig.6. Number of visits per plant against the number of floral units for each plant species grown in mixture as a function of substrate type and substrate depth. a = *Centaurea jacea*; **b** = *Lotus corniculatus*. Regressions lines are based on ANCOVA results. The different number of lines between species is due to the removal of factors that did not influence regressions, based on the simplification of the complete ANCOVA model using the Akaike Information Criterion (Table 3b). "art." stands for "artificial substrate" and "nat" stands for "natural soil".

nutrient content could alter plant-pollinator interactions through nectar sugar content, as has been shown in experimental conditions and natural ecosystems (Baude et al., 2011; Cardoza et al., 2012). There is evidence that increasing depth on green roofs increases the amount of water retained in the soil and limits the impact of drought episodes on plants in the absence of watering system (Durhman et al., 2007; Getter and Rowe, 2008; Van Mechelen, Dutoit & Hermy, 2015). This could in turn impact plant attractiveness to pollinators through increased nectar production (Petanidou et al., 1999). Similarly, although the artificial substrate had a higher water retention capacity, it dried out faster than the natural soil (Dusza et al., 2017). Possibly, drier conditions in artificial substrate, as green roofs often experience (VanWoert et al., 2005a), might have led to a reduced production of nectar and a reduced number of visits per plant. Alternatively, substrate type and depth may also affect pollinator abundance through soil habitat. For instance, deeper substrates may provide more suitable habitats for ground-nesting species or solitary bees. Likewise, the high macro-porosity of the artificial substrate might have reduced the capacity of ground-nested species or solitary bees to create a suitable habitat, preventing them to forage on the mesocosm.

4.3. Designing green roofs to enhance plant-pollinator interactions

In many urban environments, measures to promote pollination mainly focus on a single generalist pollinator species, the domesticated honey bee *Apis mellifera* (Geslin et al., 2017). In the city of Paris, where the experiment was carried out, more than 1000 hives have been installed since the first one in 1856, making a mean of 10 hives per km^2 (Ville de Paris, 2017). However, there are growing concerns and controversies about promoting honey bees instead of wild pollinators (Aebi et al., 2012; Ollerton et al., 2012), even though there is evidence that wild pollinators can ensure efficient pollination (Garibaldi et al., 2013; Garantonakis et al., 2016). Because honey bees were strongly represented and have the ability to forage from ground to roofs and from

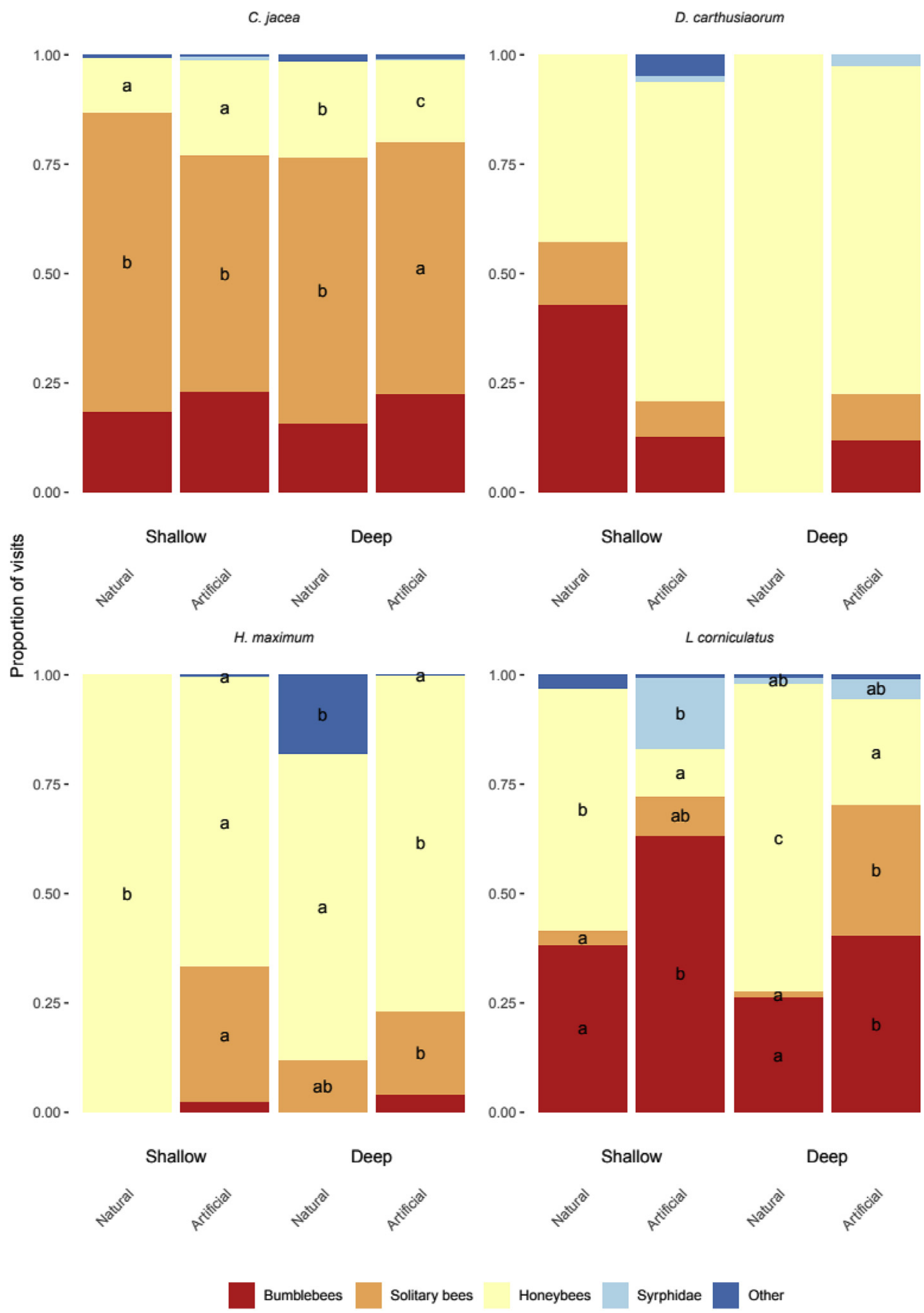

Fig. 7. Proportion of visits on each plant species grown on artificial substrate as a function of substrate type and substrate depth. Within each group of pollinators, letters indicate difference in proportions ($p < 0.05$) between treatments. Letters are only shown when there are differences between treatments.

patches to patches (Braaker et al., 2013), treatments that reduce the proportion of honey bees might be preferred. Favouring a plant community with diverse flowering phenologies and characteristics to a monoculture could have two benefits: extending pollination services for a longer period and attracting a more diverse community of pollinators (Nagase et al., 2017; Tonietto et al., 2011; Braaker et al., 2013; MacIvor et al., 2015). In addition, there is growing evidence that increasing plant species diversity when designing a green roof results in improved ecosystem multifunctionality and services (Lundholm, 2015; Dusza et al., 2017).

Overall, we found that a trade-off occurred between promoting a high number of visits using monocultures and promoting more diverse pollinator communities with mixtures. We suggest that mixing on the same roof patches of monocultures and patches of mixtures of species should help mitigating this trade-off. Testing more plant mixtures and roof configurations is needed to verify this hypothesis. In France, increasing green roof substrate depth is a current trend. Some regional or local agencies have fixed the minimum of substrate depth at 10 cm (Ville de Paris, 2012; Natureparif, 2013) in contrast to older green roof systems (2–4 cm, Monterusso et al., 2005; VanWoert et al., 2005b; Getter and Rowe, 2008). Besides, most new green roofs are currently installed on new buildings, which allow deeper substrates for a reduced economic cost compared to retrofitting. When possible, we suggest that increasing substrate depth will result in higher attractiveness to pollinators. More research is required to evaluate the effect of substrate on floral traits, such as nectar or floral display, but also on the production of fruits and seeds that are the final product of pollination. Similarly, as green roofs are expected to support biodiversity in cities, a future direction would be testing at a larger scale the effect of diverse green roof designs on the surrounding abundance and diversity of pollinators.

5. Conclusion

In this study, we showed that the choice of substrate type, substrate depth and vegetation type has an impact on both abundance and functional diversity of pollinators. Enhancing functional diversity of pollinators requires mixing plants with diverse flower morphologies and phenologies. Promoting a more abundant community of pollinators on green roofs could be achieved with deeper substrates, although we found an effect only on monocultures. We showed that although plants grown on a natural soil had less floral units, they attracted as many pollinators as plants grown on a typical green roof substrate. Further investigation is necessary to determine the mechanisms underlying the effects we found, e.g. to determine how substrate composition influences floral traits and in turn plant-pollinator interactions. This study was a first step to analyse the impact of various green roof characteristics on the attractiveness to pollinators. Future research should address the influence of these characteristics on whole green roof sustainability, the dynamics of plant diversity and the pollination of surrounding plant populations on the ground. On the long term, this line of research should allow designing rules to optimize various aspects of the impact of green roofs on pollination and pollinating communities.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Acknowledgements

We thank Vincent Peluso and Stéphane Loisel for their help during field and laboratory work. We thank the Mission Economie de la Biodiversité of CDC-Biodiversité (Caisse des Dépôts group), the Paris City Council and ICADE for funding. We are grateful to ICADE that allowed us to set up our experiment on the rooftop of their main building.

References

Aebi, A., Vaissière, B.E., vanEngelsdorp, D., Delaplane, K.S., Roubik, D.W., Neumann, P., 2012. Back to the future: Apis versus non-Apis pollination-a response to Ollerton et al. Trends Ecol. Evol. 27, 142–143.
Aguirre-gutiérrez, J., Kissling, W.D., Carvalheiro, L.G., 2016. Functional Traits Help to Explain Half-Century Long Shifts in Pollinator Distributions. vols. 1–13 Nature Publishing Group.
Albrecht, M., Duelli, P., Obrist, M.K., Kleijn, D., Schmid, B., 2009. Effective long-distance pollen dispersal in centaurea jacea. PloS One 4, e6751. https://doi.org/10.1371/journal.pone.0006751.
Arnold, S.E.J., Faruq, S., Savolainen, V., McOwan, P.W., Chittka, L., 2010. FReD: the floral reflectance database - a web portal for analyses of flower colour. PloS One 5, 1–9.
Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, E., Mitschunas, N., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Stone, G.N., Vaughan, I.P., Memmott, J., 2015. Where is the UK ' s pollinator biodiversity ? The importance of urban areas for flower- visiting insects. Proc. Roy. Soc. Med. Biol. Sci.s 282, 20142849.
Banaszak-Cibicka, W., Zmihorski, M., 2012. Wild bees along an urban gradient: winners and losers. J. Insect Conserv. 16, 331–343.
Baude, M., Leloup, J., Suchail, S., Allard, B., Benest, D., Mériguet, J., Nunan, N., Dajoz, I., Raynaud, X., 2011. Litter inputs and plant interactions affect nectar sugar content. J. Ecol. 99, 828–837.
Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in britain and The Netherlands. Science 313, 351–354.
Bjornstad, O.N., 2016. ncf: Spatial Nonparametric Covariance Functions. R package version 1.1-7. http://CRAN.R-project.org/package=ncf.
Bloch, D., Werdenberg, N., Erhardt, A., 2006. Pollination crisis in the butterfly-pollinated wild carnation *Dianthus carthusianorum*. New Phytol. 169, 699–706.
Braaker, S., Ghazoul, J., Obrist, M., Moretti, M., 2013. Habitat connectivity shapes urban arthropod communities-the key role of green roofs. Ecology 95, 1010–1021.
Brenneisen, S., 2006. Space for urban Wildlife : designing green roofs as habitats in Switzerland. Urban Habitats 4, 27–36.
Burkle, L.A., Irwin, R.E., 2010. Beyond biomass: measuring the effects of community-level nitrogen enrichment on floral traits, pollinator visitation and plant reproduction. J. Ecol. 98, 705–717.
Cardoza, Y.J., Harris, G.K., Grozinger, C.M., 2012. Effects of soil quality enhancement on pollinator-plant interactions. Psyche: J. Entomol. 8pp 2012.
Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., Roberts, S.P.M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyörgyi, H., Tscheulin, T., Westphal, C., Woyciechowski, M., Vaissière, B.E., 2009. Landscape context and habitat type as drivers of bee diversity in European annual crops. Agric. Ecosyst. Environ. 133, 40–47.
Chenot, J., Gaget, E., Moinardeau, C., Jaunatre, R., Buisson, E., Dutoit, T., 2017. Substrate composition and depth affect soil moisture behavior and plant-soil relationship on mediterranean extensive green roofs. Water 9, 817. https://doi.org/10.3390/w9110817.
Clark, M.J., Zheng, Y., 2014. Fertilizer rate influences production scheduling of sedum-vegetated green roof mats. Ecol. Eng. 71, 644–650.
Colla, S.R., Willis, E., Packer, L., 2009. Can green roofs provide habitat for urban bees (Hymenoptera: Apidae)? Cities Environ. 2, 1–12.
de Paris, Ville, 2012. Toitures végétalisées : cahiers techniques. https://apisite.paris.fr/images/120425.pdf.
de Paris, Ville, 2017. http://www.paris.fr/biodiversite.
Deguines, N., Julliard, R., de Flores, M., Fontaine, C., 2012. The whereabouts of flower visitors: contrasting land-use preferences revealed by a country-wide survey based on citizen science. PloS One 7, e45822. https://doi.org/10.1371/journal.pone.0045822.
Deguines, N., Julliard, R., de Flores, M., Fontaine, C., 2016. Functional homogenization of flower visitor communities with urbanization. Ecol. Evol. 6, 1967–1976.
Desaegher, J., Nadot, S., Dajoz, I., Colas, B., 2017. Buzz in Paris : flower production and plant – pollinator interactions in plants from contrasted urban and rural origins. Genetica. https://doi.org/10.1007/s10709-017-9993-7.
Dunnett, N., Nagase, A., Hallam, A., 2008. The dynamics of planted and colonising species on a green roof over six growing seasons 2001 – 2006 : influence of substrate depth. Urban Ecosyst. 11, 373–384.
Durhman, A.K., Rowe, D.B., Rugh, C.L., 2007. Effect of substrate depth on initial growth , coverage , and survival of 25 succulent green roof plant taxa. Hortscience 42, 588–595.
Dusza, Y., Barot, S., Kraepiel, Y., Lata, J.-C., Abbadie, L., Raynaud, X., 2017. Multifunctionality under green roof context is affected by interactions between plant species, substrate depth and substrate type. Ecol. Evol. 7, 2357–2369.
Flacher, F, Hansard, A, Motard, E, Fofana M, A, Vincent, O, Geslin, B, Dajoz, I, Raynaud, X, 2017. Does competition with wind-pollinated species alter Echium plantagineum's attractiveness to a common pollinator Bombus terrestris? Ecol. Entomol. 42, 617–628. https://doi.org/10.1111/een.12426.
Flacher, F, Raynaud, X, Hansart, A, Geslin, B, Motard, E, Verstraet, S, Bataille, M, Dajoz, I, 2020. Belowground competition induced by a wind-pollinated species influences attractiveness of an insect-pollinated plant, S. alba, to wild pollinators. AOB Plants in press.
Flacher, F., Raynaud, X., Hansart, A., Motard, E., Dajoz, I., 2015. Competition with wind-pollinated plant species alters floral traits of insect-pollinated plant species. Sci. Rep. 5, 1–10.
Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M., 2006. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. PLoS Biol. 4 0129–0135.
Fortel, L., Henry, M., Guilbaud, L., Guirao, A.L., Kuhlmann, M., Mouret, H., Rollin, O., Vaissière, B.E., 2014. Decreasing abundance, increasing diversity and changing structure of the wild bee community (hymenoptera: anthophila) along an urbanization gradient. PloS One 9.
Galyean, M.L., Wester, D.B., 1 octobre 2010. Comparison of multinomial and binomial proportion methods for analysis of multinomial count data. J. Anim. Sci. 88 (10), 3452–3463. https://doi.org/10.2527/jas.2010-2868.
Garantonakis, N., Varikou, K., Birouraki, A., Edwards, M., Kalliakaki, V., Andrinopoulos, F., 2016. Comparing the pollination services of honey bees and wild bees in a watermelon field. Sci. Hortic. 204, 138–144.
Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipolito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339, 1608–1611.
Geslin, B., Gauzens, B., Thébault, E., Dajoz, I., 2013. Plant pollinator networks along a gradient of urbanisation. PloS One 8, 1–14.
Geslin, B., Le Féon, V., Folschweiller, M., Flacher, F., Carmignac, D., Motard, E., Perret, S., Dajoz, I., 2016. The proportion of impervious surfaces at the landscape scale structures wild bee assemblages in a densely populated region. Ecol. Evol. 6, 6599–6615.
Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Fontaine, C., Henry, M., Ropars, L., Rollin, O., Thébault, E., Vereecken, N.J., 2017. Massively introduced managed species and their consequences for plant–pollinator interactions. Adv. Ecol. Res. 57, 147–199.
Getter, K.L., Rowe, D.B., 2008. Media depth influences Sedum green roof establishment. Urban Ecosyst. 11, 361–372.
Gorden, N.L.S., Adler, L.S., 2013. Abiotic conditions affect floral antagonists and mutualists of Impatiens capensis (Balsaminaceae). Am. J. Bot. 100, 679–689.
Hoffmann, M.M., Renner, S., 2017. Bee species recorded between 1992 and 2017 from green roofs in Asia, Europe, and North America, with key characteristics and open research questions. Apidologie. https://doi.org/10.1007/s13592-017-0555-x.
Kadas, G., 2006. Rare invertebrates colonizing green roofs in london. Urban Habitats 4, 66–86.

Kanechi, M., Fujiwara, S., Shintani, N., Suzuki, T., Uno, Y., 2014. Performance of herbaceous Evolvulus pilosus on urban green roof in relation to substrate and irrigation. Urban For. Urban Green. 13, 184–191.
Kratschmer, S., Kriechbaum, M., Pachinger, B., 2018. Buzzing on top: linking wild bee diversity, abundance and traits with green roof qualities. Urban Ecosyst. 21, 429–446.
Ksiazek, K., Fant, J., Skogen, K., 2012. An assessment of pollen limitation on Chicago green roofs. Landsc. Urban Plann. 107, 401–408.
Lata, J., Dusza, Y., Abbadie, L., Barot, S., Carmignac, D., Gendreau, E., Kraepiel, Y., Mériguet, J., Motard, E., Raynaud, X., 2017. Role of substrate properties in the provision of multifunctional green roof ecosystem services. Appl. Soil Ecol.
Lenth, R., 2015. lsmeans: Least-Squares Means. R Package Version 2. pp. 20–23.
Lu, J., Yuan, J., Yang, J., Chen, A., Yang, Z., 2015. Effect of substrate depth on initial growth and drought tolerance of Sedum lineare in extensive green roof system. Ecol. Eng. 74, 408–414.
Lundgren, R., Lazaro, A., Totland, O., 2015. Effects of experimentally simulated pollinator decline on recruitment in two European herbs. J. Ecol. 103, 328–337.
Lundholm, J.T., 2015. Green roof plant species diversity improves ecosystem multifunctionality. J. Appl. Ecol. 52, 726–734.
Macivor, J.S., Lundholm, J., 2011. Insect species composition and diversity on intensive green roofs and adjacent level-ground habitats. Urban Ecosyst. 14, 225–241.
MacIvor, J.S., Ruttan, A., Salehi, B., 2015. Exotics on exotics: pollen analysis of urban bees visiting Sedum on a green roof. Urban Ecosyst. 18, 419–430.
Madre, F., Vergnes, A., Machon, N., Clergeau, P., 2013. A comparison of 3 types of green roof as habitats for arthropods. Ecol. Eng. 57, 109–117.
Madre, F., Vergnes, A., Machon, N., Clergeau, P., 2014. Green roofs as habitats for wild plant species in urban landscapes: first insights from a large-scale sampling. Landsc. Urban Plann. 122, 100–107.
Matteson, K.C., Grace, J.B., Minor, E.S., 2012. Direct and indirect effects of land use on floral resources and flower-visiting insects across an urban landscape. Oikos 122, 682–694.
McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. Biol. Conserv. 127, 247–260.
McKinney, M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. Urban Ecosyst. 11, 161–176.
Monterusso, M.A., Rowe, D.B., Rugh, C.L., 2005. Establishment and persistence of sedum spp . and native taxa for green roof applications. Hortscience 40, 391–396.
Nagase, A., Dunnett, N., Choi, M., 2017. Investigation of plant growth and flower performance on a semi-extensive green roof. Urban Forestry & Urban Greening.
Natureparif, 2013. Réaliser des toitures végétales favorables à la biodiversité. http://www.Natureparif.fr/attachments/Documentation/livres/Toitures-vegetalisees.pdf.
Oberndorfer, E., Lundholm, J., Bass, B., Coffman, R.R., Doshi, H., Dunnett, N., Gaffin, S., Köhler, M., Liu, K.K.Y., Rowe, B., 2007. Green roofs as urban ecosystems : ecological structures, functions, and services. Bioscience 57, 823–833.
Ollerton, J., Price, V., Armbruster, W.S., Memmott, J., Watts, S., Waser, N.M., Totland, Ø., Goulson, D., Alarcón, R., Stout, J.C., Tarrant, S., 2012. Overplaying the role of honey bees as pollinators: a comment on Aebi and Neumann (2011). Trends Ecol. Evol. 27, 141–142.
Ondoño, S., Bastida, F., Moreno, J.L., 2014. Microbiological and biochemical properties of artificial substrates: a preliminary study of its application as Technosols or as a basis in Green Roof Systems. Ecol. Eng. 70, 189–199.
Ondoño, S., Martínez-Sánchez, J.J., Moreno, J.L., 2015. Evaluating the growth of several Mediterranean endemic species in artificial substrates: are these species suitable for their future use in green roofs? Ecol. Eng. 81, 405–417.
Pellissier, V., Muratet, A., Verfaillie, F., Machon, N., 2012. Acta Oecologica Pollination success of Lotus corniculatus (L.) in an urban context. Acta Oecol. 39, 94–100.
Petanidou, T., Goethals, V., Smets, E., 1999. The effect of nutrient and water availability on nectar secretion and nectary structure of the dominant Labiatae species of phrygana. Syst. Geogr. Plants 68, 233–244.
Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353.
R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Rowe, D.B., Getter, K.L., Durhman, A.K., 2012. Effect of green roof media depth on Crassulacean plant succession over seven years. Landsc. Urban Plann. 104, 310–319.
Snow, A.A., Whigham, D.F., 1989. Costs of flower and fruit production in Tipularia discolor (Orchidaceae). Ecology**70** 1286–1293.
Steffan-Dewenter, I., Nzenberg, U.M., Rger, C.B., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 1421–1432.
Thuring, C.E., Berghage, R.D., Beattie, D.J., 2010. Green roof plant responses to different substrate types and depths under various drought conditions. Hortechnology 20, 395–401.
Tonietto, R., Fant, J., Ascher, J., Ellis, K., Larkin, D., 2011. A comparison of bee communities of Chicago green roofs, parks and prairies. Landsc. Urban Plann. 103, 102–108.
Van Mechelen, C., Dutoit, T., Hermy, M., 2014. Mediterranean open habitat vegetation offers great potential for extensive green roof design. Landsc. Urban Plann. 121, 81–91. https://doi.org/10.1016/j.landurbplan.2013.09.010.
Van Mechelen, C., Dutoit, T., Hermy, M., 2015. Adapting green roof irrigation practices for a sustainable future: a review. Sustain. Cities Soc. 19, 74–90.
VanWoert, N.D., Rowe, D.B., Andresen, J.A., Rugh, C.L., Fernandez, R.T., Xiao, L., 2005a. Green roof stormwater retention: effects of roof surface, slope, and media depth. J. Environ. Qual. 34, 1036–1044.
VanWoert, N.D., Rowe, D.B., Andresen, J.A., Rugh, C.L., Xiao, L., 2005b. Watering regime and green roof substrate design affect sedum plant growth. Hortscience 40, 659–664.
Vijayaraghavan, K., 2016. Green roofs: a critical review on the role of components, benefits, limitations and trends. Renew. Sustain. Energy Rev. 57, 740–752.
Winfree, R., Griswold, T., Kremen, C., 2007. Effect of human disturbance on bee communities in a forested ecosystem. Conserv. Biol. 21, 213–223.