A comparison of 3 types of green roof as habitats for arthropods

Frédéric Madre*, Alan Vergnes, Nathalie Machon, Philippe Clergeau

Museum National d’Histoire Naturelle, Département d’Ecologie, UMR CERSP, Paris, France

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ABSTRACT

In an inexorably urbanizing world, green roofs could be an interesting tool to conciliate the greening of cities with ecological services. Studies on a large number of sites are necessary to understand the importance of environmental variables, especially how the type of vegetation affects the green roof biodiversity.

We sampled several arthropods (spiders, true bugs, beetles and hymenopterans) from buildings covered by green roofs in 115 sites across northern France. We considered 3 types of green roofs with diverse vegetal structures: muscinal (moss/sedum – M) roofs, herbaceous (moss/sedum and meadow – H) roofs and arbustive (moss/sedum, meadow and shrub – A) roofs.

The species richness and the abundance of most of the taxa were significantly higher on A roofs, which displayed more complex vegetation. Predominantly common species comprised the arthropod communities. However, xero-thermophilic species and species from sandy and rocky habitats were also present because green roofs could serve as habitat analogs of those dry natural habitats. Except for hymenopterans, we did not observe a difference in the functional composition of communities; however, the taxonomic composition of spider communities was significantly affected by the green roof type. The surrounding environment and other local variables exhibited a minor influence on the composition, abundance and richness of the arthropods. We revealed a major role for the vegetal structures in arthropod communities and the ability of green roofs to enhance urban biodiversity.

* Corresponding author at: Muséum National d'Histoire Naturelle, Département d'Ecologie, UMR CERSP, 55 rue Buffon, 75005 Paris, France. Tel: +33 1 4407 95765; fax: +33 1 4407 93835.

E-mail addresses: madre@mnhn.com (F. Madre), alan.vergnès@gmail.com (A. Vergnes), machon@mnhn.fr (N. Machon), clergeau@mnhn.fr (P. Clergeau).

1. Introduction

With more than half of the human population residing in cities, which is projected to rise to 70% in 2030 (UNFPA, 2011), urban areas detrimentally invade natural landscapes (Fischer and Lindenmayer, 2007), thereby impacting the entire planet (Grimm et al., 2008). Policy makers, urban planners, architects and, more recently, naturalists must (i) fulfill the basic needs of urban dwellers, such as housing, health and education (UN-HABITAT, 2008), and (ii) limit the major negative effects of urbanization by enhancing quantity and quality of natural spaces in cities. These two challenges may be difficult to reconcile but in fact they are highly interdependent. The presence of biodiversity and the services it provides could contribute to the basic human needs, such as health or well-being (Costanza et al., 1998; Dearborn and Kark, 2010; Bai et al., 2012), and greening cities and especially of buildings could help accomplish biodiversity (Jim, 2004; UN-HABITAT, 2008).

Green roofs (roofs with a substrate and a vegetated surface) may be one of the most promising ecological engineering techniques to increase green surfaces (Mitsch, 2012). Restoring habitats by removing existing infrastructure is complex due to the strong land-use conflicts in cities (e.g., housing and business pressures), thus creating habitats on existing or new buildings may be a tenable compromise (Tzoulas et al., 2007).

Historically, green roofs have been implemented for the technical benefits they provide to buildings, such as roof membrane longevity improvement, storm-water management and summer cooling (Oberndorfer et al., 2007). Furthermore, buildings with rooftop-gardens possess esthetic and recreational values that enhance their economic value (Liu, 2002). These benefits explain the increased presence of green roofs worldwide. For example in France, from 100,000 m² to 1,000,000 m² of green roofing has been implemented yearly for the past ten years according to ADIVET (French association of green roofing companies).

The ecological values of green roofs, such as providing shelter for numerous organisms, have only recently piqued the interest of urban ecologists, as they could shelter many organisms. Some birds have already been observed nesting in green roofs, such as the northern lapwing (Vanellus vanellus) in Switzerland (Baumann, 2006) and the black redstart (Phoenicurus ochruros) in England (Grant, 2006). However, green roofs may be even more important
for other organisms, such as arthropods, that need small habitats to maintain viable populations (Gaston et al., 1998). Even if urban dwellers harbor a generally negative perception of arthropods (Kim, 1993), arthropods remain “the little things that run the world” (Wilson, 1987). They represent a major component of the ecosystems and are responsible for numerous functions and services such as decomposition, pollination and biological control. Furthermore, they are highly threatened by urbanization (Hunter, 2002; McKinney, 2008).

Previous studies have stressed the importance of the presence of arthropod communities on green roofs. A community richness and composition equivalent to those of other urban green spaces were observed (Colla, 2009; Maclvor and Lundholm, 2011a; Ksiazek et al., 2012). Even rare arthropod species were observed (Jones, 2002; Brenneisen, 2006; Kadas, 2006), which piqued the potential interest in green roofs, particularly ones with structured vegetation, for conservation and ecosystem services in urban areas (Hunter and Hunter, 2008) where “people live and work” (Miller and Hobbs, 2002). The potential is strengthened by the important surface available for the settling of green roofs, which has been estimated at over 32% of the horizontal 2D surface in some cities according to Frazer (2005). These pioneer studies assessed environmental factors that could affect the distribution of species on green roofs but, unfortunately suffered from a low number of sampled sites (approximately ten per study).

Extensive and simple intensive greening (The Roof Greening Working Group, 2002) is technically divided into three main solutions that place the vegetal structures as the principal factors that change with different vegetal palettes planted at different substrate depths (Madre et al., 2012). Three vegetation layers are currently planned on buildings. They range from a unique low strata comprised of bryophytes (mosses) and succulent plants from the Sedum genus, typically termed as extensive roofs (M type), to more complex roofs with higher vegetal structures such as herbs (H type) and even shrubs (A type), typically termed as simple intensive roofs. These types are considered as three different levels of structural vegetation complexity.

In this study, we sampled arthropods from numerous sites (115 roofs in northern France) in order to assess whether the previous trends are representative and to identify factors that shape the arthropod biodiversity on green roofs, including the surrounding environment and other local variables, particularly the difference between green roof types (hereafter named the GR type effect).

By studying four taxa of arthropods, we answered the following questions:

1. Does the GR type effect supported the “structural complexity hypothesis” that assumes that structurally diverse habitats (with different vegetation layers) yield more niches, thereby increasing the diversity and abundance of animal communities (MacArthur and MacArthur, 1961; Tews et al., 2004), especially arthropods (Southwood et al., 1979; Langellotto and Denno, 2004; Mормul et al., 2011)?

2. Is there a GR type effect on the taxonomic arthropod composition?

3. Is there a GR type effect on the ecological attributes of arthropod communities, such as the dispersal capabilities and habitat affinities?

4. Are the arthropod communities affected by other environmental variables, such as the green roof area, building height, plant species richness, plant coverage and potential surrounding habitats?

Finally, we discussed our results and their impacts on the fields of urban planning and ecological engineering.

2. Materials and methods

2.1. Sampling design and study area

Following a green roof typology based on a significant proportion of the maximal vegetal strata (Madre et al., 2012, Supplementary Fig. 1), we considered three types of green roofs:

1. The muscinal roof (M) is primarily composed of low-development pioneer plants such as bryophytes (mosses) or vascular creeping plants from the Sedum genus such as Sedum album, Sedum spurium or Sedum sexangulare. This type refers to extensive greening and excludes roofs that are covered by herbaceous plants on more than 20% of their surfaces.

2. The herbaceous (H) roof is composed of the understory plants of the M roof and is covered by herbaceous plants (graminaceous and other non-woody plants such as Festuca glauca, Petrorhagia saxifraga or Allium schoenoprasum) on more than 20% of its surface.

3. The arbustive (A) roof is the most diverse type, composed of the previous strata and is covered of woody plants (shrubs such as Lavandula angustifolia, Cotoneaster franchetii or Pinus mugo) on more than 20% of its surface.

These three types correspond to different technical solutions proposed by green roofing companies, such as “Toundra,” “Pampa” and “Garrigue” (scrubland) systems by Sopranature® for example.

One hundred and fifteen green roofs were sampled, selected from green roofing companies’ databases according to their technical characteristics. A representative number of each roof type was sampled: 45 M roofs, 38 H roofs and 32 A roofs. As M roofs represent the majority of the green roofs currently implemented (estimated at 95% of green roofs in France), we studied a large area to obtain a representative sample for each type. The study was performed in northern France in the spring of 2011. The sites are located along a west–east transect of 900 km (from −4.483 to 7.787 latitude in decimal degrees) and a north–south gradient of 300 km (from 49.758 to 46.752 longitude in decimal degrees) (Fig. 1A). In this area, the landscape is primarily dominated by agricultural land uses but the green roofs are predominantly located in and around the cities (Fig. 1B).

2.2. Arthropod sampling and ecological attributes

In this paper, we adopted a multi-taxa approach and targeted four arthropod taxa: spiders (Araneae), beetles (Coleoptera), true bugs (Heteroptera) and hymenopterans (Hymenoptera: ants, wasps and bees). These taxa encompass a broad range of functional aspects and especially different trophic levels: predators for spiders and predominantly phytophageous for true bugs (Heteroptera), beetles (Coleoptera) and hymenopterans. Our two constraints were (i) to sample a high number of sites and (ii) to sample all of the different taxa on the roof, including the ground level and the different vegetation layers. Thus, we adopted a standardized hand-sampling that has been shown to be less time-consuming and less labor-intensive than other methods such as pitfall traps (Gotelli et al., 2011). We standardized the hand-sampling method for both time and area to allow for a quantitative comparison between sites (Churchfield et al., 1991; Gotelli et al., 2011). For each site, we captured the arthropods in pill bottles for 10 min in a fixed band width of 2 m along a 20-m transect. Arthropods were captured from plants from all vegetal layers simultaneously. The sampling was conducted from 11 April to 7 June 2011.

The individuals were identified at a species level. Juveniles and larvae, which could not be identified at this level, were excluded from the analyses (n = 21).
arthropods.

2.3. Environmental variables

In addition to the GR type effect, we studied a set of environmental variables recorded in and around each roof, respectively at the local (i.e., green roof characteristics) and the landscape scale (i.e., land cover in a 2-km buffer around each site).

At the local scale, we selected two physical building characteristics: the surface area of the green roof and its height. The substrate depth and the age of the green roofs were excluded from the analysis as these variables were strongly correlated with the type of green roof (see Supplementary Table 3). For the biological characteristics, an exhaustive list of vascular plants was established and we considered the total plant species richness (SR_plant). We have also estimated the vascular plant coverage for each green roof (Plant_cover), as it varies greatly from one site to another and may influence arthropod communities. All of these variables were measured after the arthropods were sampled to avoid observer disturbance.

At the landscape scale, we measured the percentage of habitats (i.e., Corine Land Cover classes) in a 2-km radius around each site (Hab) using ArcGIS 9.3. Numerous studied taxa harbor important dispersal capabilities (air dispersal of several kilometers for spiders; Bell et al., 2005), so the size of the buffer was selected to include distant habitats that could colonize green roofs. From the 44 classes from the Corine Land Cover database (Bossard et al., 2006), we selected 30 classes that could be considered as potential habitats for arthropods that reside on green roofs: open and semi-open natural habitats, such as grasslands, sandy beaches and dunes, and their analogs, such as crops, urban parks and quarries (Tropek et al., 2010). Details are given in Supplementary Table 2.

2.4. Statistical analysis

The species richness, their abundance and the taxonomic and functional composition of the communities were investigated all of the arthropods and all four taxa. We considered the spatial autocorrelation (hereafter SAC) because "locations close to each other exhibit more similar values than those further apart" (Dormann et al., 2007). SAC originates from spatially structured data, which makes an accurate detection and measurement of biological responses difficult when they remain in the model residuals (Legendre et al., 2002). Moreover, these methods allow for the correction of the potential effects of the biogeographical processes (expressed along latitudinal and longitudinal gradients). With this approach, the pure effects of the other environmental variables can be properly studied.

Analyses were computed with the R 2.13.1 software (R Development Core Team, 2011).

2.4.1. Species richness and abundance

To analyze the effects of the environmental variables described above on species richness and abundance, we used Generalized Linear Models (GLMs) corrected for spatial autocorrelation. The GLMs were computed with a Poisson distribution error, which is particularly suited for the nature of count data (Crawley, 2009). Using a Moran’s I test, we assessed for the SAC in the model residuals every 0.1 km between 0.1 and 6 km. When SAC was detected, an autocovariate was computed and integrated in the model, as proposed by Dormann et al. (2007). Moran’s I tests were computed with the library ncf (Bjornstad, 2012) and the autocovariate with the library spdep (Bivand, 2012). The results of Moran’s I test and autocovariates are detailed in Supplementary Fig. 1.

2.4.2. Taxonomic and functional community compositions

We analyzed the effects of the variables on the taxonomic composition of the communities using a distance-based partial Redundancy-Analysis (db-RDA). As the constrained ordination method, the db-RDA is an extension of unconstrained ordination (principal component analysis or PCA in our case). The db-RDA explicitly models response variables as a function of explanatory variables (the constraints) (Zuur et al., 2007). The db-RDA is a constrained ordination method that allows for the use of non-Euclidian distances between communities (Legendre and Gallagher, 2001; Anderson and Willis, 2003). Here, we used an absence/presence matrix with a Jaccard distance (Legendre and Gallagher, 2001) because it places more importance on the double presence (the presence of a species in different sites) than the double absence (Zuur et al., 2007). We computed a Hellinger transformation prior to analyze to analysis to limit the importance of highly frequent species (Legendre and Gallagher, 2001). Empty sites (n = 29) were excluded from the analysis and all species were considered in the analysis. To correct for SAC, we computed a model with all of the variables as constrained effects and the geographical coordinates of sites (x_coord and y_coord) were considered as partial effects (Legendre and Gallagher, 2001; Wagner and Fortin, 2005). Analyses were computed with the capsule function of the vegan library (Oksanen et al., 2011).
The functional community compositions were computed using a partial Redundancy Analysis on a community weighted trait matrix (CWM). In CWM, the mean of the values present in the community are weighted by the relative abundance of taxa bearing each value (Lavorel et al., 2008). CWM is an efficient functional index to summarize the effects of environmental selection by detecting variations in mean trait values within communities, which are presented in Supplementary Table 1 (Ricotta and Moretti, 2011).

The statistical significance of the entire model and of each variable (marginal tests) were evaluated with Monte-Carlo’s permutation tests (n = 999).

3. Results

We captured 290 individuals from 66 species. We captured 50 individual spiders, 51 beetles, 26 true bugs and 163 hymenopterans (103 of which were ants) of 21, 11, 10 and 24 species, respectively. The most abundant species were the ant Lasius niger (27.48% of the total abundance and present in 32 sites), the beetle Cocinella septempunctata (7.90% in 15 sites), the hymenopteran Bombus lapidarius (6.52% in 15 sites) and the true bug Pyrrhocoris apterus (5.49% in 15 sites). The most frequent species were the same species, in the same order. Only two beetle species were considered as invasive in the sample area, Harmonia axyridis and Chrysomelina americana.

3.1. Green roofs characteristics

The landscape surrounding the green roof sites was predominately urban with a proportion of potential habitats for arthropods ranging from 0% to 87% (mean: 22 ± 23%) in a 2-km buffer. The green roofs surface area was highly variable (mean: 415 ± 518 m²). The building height ranged from soil level (0 m) to 25 m (mean: 5.7 ± 4.7 m). The vascular plant species richness varied from 6 to 105 species (mean: 26 ± 14). The vascular plant coverage of green roofs ranged from 20% to 100% (mean: 77 ± 19%).

Table 1

Results of Generalized Linear Models (GLM) demonstrating the differences between A roofs and H and M roofs and the effects of other environmental variables on species richness (A) and abundance (B). For species richness and abundance, β and SE were transformed into mean species richness per trap and mean abundance with SE per trap using an exponential function.

<table>
<thead>
<tr>
<th>(A)</th>
<th>Total</th>
<th>Spiders</th>
<th>Beetles</th>
<th>True bugs</th>
<th>Hymenopterans</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>2.2 (1.51)*</td>
<td>2.29 (2.39)</td>
<td>1.38 (2.69)</td>
<td>50.91 (6.69)*</td>
<td>2.03 (1.79)</td>
</tr>
<tr>
<td>A/H-type</td>
<td>−1.34 (1.19)*</td>
<td>−1.65 (1.45)*</td>
<td>−1.95 (1.49)*</td>
<td>−1.3 (2.1)</td>
<td>−1.16 (1.26)</td>
</tr>
<tr>
<td>H/M-type</td>
<td>−0.61 (0.19)*</td>
<td>−0.43 (0.41)</td>
<td>−0.85 (0.51)*</td>
<td>0.57 (0.62)</td>
<td>−0.80 (0.28)*</td>
</tr>
<tr>
<td>A/M-type</td>
<td>−2.44 (1.21)**</td>
<td>−2.61 (1.49)**</td>
<td>−4.26 (1.63)**</td>
<td>−1.28 (1.88)</td>
<td>−2.77 (1.32)**</td>
</tr>
<tr>
<td>Hab</td>
<td>1 (1)</td>
<td>1.01 (1.01)</td>
<td>1.01 (1.01)</td>
<td>1.01 (1.01)</td>
<td>1.01 (1.01)</td>
</tr>
<tr>
<td>Surface</td>
<td>1 (1)</td>
<td>1 (1)</td>
<td>1 (1)</td>
<td>1 (1)</td>
<td>1.01 (1.01)</td>
</tr>
<tr>
<td>Sr,plant</td>
<td>1 (1.01)</td>
<td>1 (1.01)</td>
<td>−1.02 (1.02)</td>
<td>1.01 (1.02)</td>
<td>1.01 (1.01)</td>
</tr>
<tr>
<td>Plant_cover</td>
<td>1.26 (1.48)</td>
<td>1.75 (2.23)</td>
<td>1.27 (2.51)</td>
<td>46.53 (6.05)</td>
<td>1.08 (1.72)</td>
</tr>
<tr>
<td>Height</td>
<td>−1.15 (1.12)</td>
<td>−1.84 (1.28)*</td>
<td>−1.39 (1.27)</td>
<td>−1.99 (1.57)</td>
<td>1.17 (1.19)</td>
</tr>
<tr>
<td>Autoco.</td>
<td>1.03 (1.06)</td>
<td>−1.27 (1.54)</td>
<td>−1.22 (1.54)</td>
<td>−407.48 (29.67)*</td>
<td>1.35 (1.12)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>(B)</th>
<th>Total</th>
<th>Spiders</th>
<th>Beetles</th>
<th>True bugs</th>
<th>Hymenopterans</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>3.10 (1.43)*</td>
<td>1.25 (2.28)</td>
<td>2.35 (2.34)</td>
<td>−50.88 (6.70)*</td>
<td>1.16 (1.62)</td>
</tr>
<tr>
<td>A/H-type</td>
<td>−1.62 (1.15)*</td>
<td>−1.33 (1.43)</td>
<td>−2.23 (1.40)*</td>
<td>−1.29 (2.10)</td>
<td>−1.57 (1.19)*</td>
</tr>
<tr>
<td>H/M-type</td>
<td>−0.66 (0.17)**</td>
<td>−0.35 (0.36)</td>
<td>−1.03 (0.50)*</td>
<td>0.42 (0.50)</td>
<td>−1.05 (0.25)**</td>
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<tr>
<td>A/M-type</td>
<td>−3.13 (1.17)**</td>
<td>−1.88 (1.45)**</td>
<td>−6.28 (1.58)**</td>
<td>−1.29 (1.87)</td>
<td>−4.49 (1.27)**</td>
</tr>
<tr>
<td>Hab</td>
<td>1.00 (1.00)</td>
<td>1.01 (0.01)</td>
<td>−1.01 (0.01)</td>
<td>−1.02 (1.01)</td>
<td>1 (1)</td>
</tr>
<tr>
<td>Surface</td>
<td>1.00 (1.00)*</td>
<td>1 (1)</td>
<td>1 (1)</td>
<td>1 (1)</td>
<td>1 (1)</td>
</tr>
<tr>
<td>Sr,plant</td>
<td>1 (1)</td>
<td>1.01 (0.01)</td>
<td>−0.03 (0.01)</td>
<td>1.01 (1.02)</td>
<td>1 (1)</td>
</tr>
<tr>
<td>Plant_cover</td>
<td>1.85 (1.39)*</td>
<td>−1.04 (2.13)</td>
<td>0.56 (0.81)</td>
<td>46.6 (6.03)*</td>
<td>1.62 (1.54)</td>
</tr>
<tr>
<td>Height</td>
<td>−1.85 (1.10)</td>
<td>−1.61 (1.25)</td>
<td>−0.32 (0.2)</td>
<td>−1.98 (1.56)</td>
<td>1.27 (1.13)*</td>
</tr>
<tr>
<td>Autoco.</td>
<td>−0.03 (1.04)</td>
<td>1.06 (1.30)</td>
<td>−3.15 (2.32)</td>
<td>−409.07 (29.58)*</td>
<td>−1.05 (1.10)</td>
</tr>
</tbody>
</table>

* Significance level (p < 0.1).
** Significance level (p < 0.05).
*** Significance level (p < 0.001).
than in H or M roofs ($\beta(A/H) = -3.13 \pm 1.17$, $p < 0.01$ and $\beta(A/M) = -1.62 \pm 1.15$, $p < 0.001$, respectively) and higher abundances in H roofs than in M roofs ($\beta(H/M) = -0.66 \pm 1.17$, $p < 0.001$). We also observed a significant positive effect of the roof surface ($\beta = 1.00 \pm 1.00$, $p < 0.01$). For beetles, we observed a GR type effect, with abundances significantly higher in A roofs than in M roofs or in H roofs ($\beta(A/M) = -6.28 \pm 1.58$, $p < 0.001$ and $\beta(A/H) = -2.23 \pm 1.40$, $p < 0.01$, respectively) and in H roofs than in M roofs ($\beta(H/M) = -1.03 \pm 0.50$, $p < 0.05$). For true bug abundances, we noted a positive effect of the plant coverage ($\beta = 46.6 \pm 6.03$, $p < 0.05$). Hymenopterans were significantly more abundant in A roofs than in H or M roofs ($\beta(A/H) = -1.57 \pm 1.19$, $p < 0.01$ and $\beta(A/M) = -4.49 \pm 1.27$, $p < 0.001$, respectively) and in H roofs than in M roofs ($\beta(H/M) = -1.05 \pm 0.25$, $p < 0.001$).

### 3.3. Taxonomic community compositions

The spider communities were significantly structured by the GR type effect ($p < 0.01$, Table 2). The different GR types were distributed along the first axis and the second axis (Fig. 2). A roofs were characterized by species such as Mangora acalypha, Heliophanus flavipes and Theridion impressum. H roofs were characterized by Xysticus acerbus, Heliophanus kochii, Meioneta rarestris and Pardosa proxima. M roofs were characterized by fewer species, including Heliophanus cupreus, Heliophanus tribulusus, Euephyrus herbigrada, Xysticus cristatus and Zilla diida.

Marginal tests on the environmental variables demonstrated that beetle communities were significantly correlated with building height ($p < 0.01$). Along axis 1 (Fig. 2), low roofs were characterized by Harmonia axyridis and Chrysomelidae americana whereas high roofs were dominated by Coccinella septempunctata.

We did not observe any significant effects for true bugs, despite an important constrained inertia (32.24% of total inertia, Table 2). The conditional effects (latitudinal and longitudinal gradients) comprised 20.12% of the total inertia.

For hymenopterans, the full model explained 17.99% of the total inertia and was significant ($p < 0.05$, Table 2). Marginal tests on the environmental variables revealed that the building height was significant ($p < 0.01$). Along axis 1 (Fig. 2), lower roofs were characterized by two ant species, Lasius niger and Formica cunicularia whereas higher roofs were associated with Bombus lapidarius.

### 3.4. Functional traits

Among the 66 inventoried species, 58 species (88%) were able to fly and only 8 species (12%) were not.

Twenty-nine species (44%) were identified as generalist species, 20 species (30%) were thermophilic and 17 species (26%) were specialists of open xero-thermophilic habitats.

Results of the CWM analysis did not reveal significant effects for the studied variables except for hymenopterans. For this taxon, we observed a significant effect for the surrounding habitat on the open xero-thermophilic habitat affinity trait ($p < 0.001$)

### 4. Discussion

By sampling more than 100 sites, we identified that the species richness and the arthropod abundance were higher in A roofs, which corroborated the “structural complexity hypothesis”. The arthropod communities were predominantly comprised of common species, but some xeric and interesting species were also observed, which further underscored an importance of employing green roofs to enhance urban biodiversity.
4.1. Positive effect of the GR type on specific richness and abundance

For beetles, hymenopterans and spiders, we observed that A roofs with structurally complex vegetation exhibited a higher species richness than M roofs with low vegetation limited by the substrate depth. This result is consistent with the “structural complexity hypothesis” (Southwood et al., 1979), and the benefits of structurally complex vegetation on species richness are well-documented (reviewed by Tews et al., 2004). These results are also consistent with studies conducted on beetles (Columbia-Garcia et al., 1997) and spiders (Greenstone, 1984; Dennis et al., 1998; Carvalho et al., 2011). There is a paucity of data for hymenopterans, except for ants (Bestelmeyer and Wiens, 2001), which have not been analyzed separately due to the low number of species (see Supplementary Table 1). Similar to what was observed for two true bug families (Miridae and Nabidae) by Dennis et al. (1998), we did not detect any GR type-mediated significant effects on this taxon. The low number of species captured (ten species), which limited the range of variability and precluded proper analysis, could explain this result.

We demonstrated a positive relationship between the GR type and arthropod abundance, which is also consistent with the “structural complexity hypothesis”. Notably, the biomass of the vegetation is known to increase with structural complexity. This relates to the “consumer rarity hypothesis”, which assumes that the vegetation biomass positively correlates with arthropod abundance. Vegetation represents the first level of numerous food webs, so increasing the vegetation biomass influences trophic levels higher up in the food web (phytophageous and predators) by a bottom-up control (Murdoch et al., 1972; Siemann, 1998; Haddad et al., 2001). Previous works on spiders (Borges and Brown, 2001), phytophageous arthropods (Krass and Tscharnkte, 2002) or both (Dennis et al., 1998) demonstrated a positive relationship between structural complexity and abundance. In our study, the abundance of all the groups, except true bugs, was correlated with the GR type. Indeed, A roofs sheltered more abundant arthropod communities than M roofs or H roofs, as previously suggested by Coffman (2007).

Taken together, our results confirmed previous studies on green roofs (Bremsen, 2006; Kadas, 2006; Coffman, 2007), although these studies sampled only a few sites.

4.2. Taxonomic and functional composition of arthropod communities: does the type of green roof matter?

When considering each taxon separately, only the composition of spider communities was significantly shaped by the GR type. Indeed, the different spider species are clearly distributed according to their hunting behavior along the vertical layers of vegetation (Gibson et al., 1992; McNett and Rypstra, 2000). Some cursorial species, such as the jumping spiders (Salticidae) do not use a web to prey but instead run on the ground and the lower layers of vegetation. In our study, some jumping spiders like Heliothrips spp. were frequently observed in all types of green roofs, even M roofs. In contrast, orb web spiders need higher layers of vegetation, with a more complex architecture (branch, leaves,
etc) to build large interception webs (McNett and Rypstra, 2000). Consequently, Mangora acacphila associated with A roofs.

The functional composition of communities was poorly explained by the environmental variables. We observed a low dispersal variability, as the majority of the identified species were able to fly. This result was not surprising given that the green roofs should be less accessible than other green spaces at the ground level, as proposed by Brenneisen (2006). For the habitat trait, arthropod communities were comprised of a mix of generalist species and species unique to thermophilous and xero-thermophilic habitats. Only hymenopterans were affected by the surrounding environment for this ecological attribute. Hymenopteran communities correlated with habitat characteristics at a landscape scale, consistent with the results of Tonietto et al. (2011) for bee communities.

The most abundant and frequent species from green roofs are relatively common in Palaeartic areas and are observed frequently in urban areas and other highly modified landscapes. For example, L. niger (the black garden ant), the most frequent and abundant species, benefits from an association with human activities and is highly abundant in European cities (Sliipinski et al., 2012). However, 17 species thrive in xero-thermophilous habitats observed in green roofs with harsh and dry conditions. Green roofs are characterized by more extreme abiotic conditions (Obendorfer et al., 2007), such as moisture stress, severe drought, high light, wind and temperature intensities, than ground-level habitats. Moreover, the substrate is too thin to permit animals to retreat to damper areas during dry episodes (Brenneisen, 2006). In abiotic conditions, green roofs appear more equivalent to highly dry natural habitats on shallow soils, such as grasslands and rocky and sandy habitats (Grant, 2006), than other green spaces at ground levels such as lawns. The presence of xero-thermophilic species validates the premise that green roofs could be considered as habitat analogs of dry natural habitats (Lundholm and Richardson, 2010). Here, we demonstrated a trend observed in previous studies (Jones, 2002; Kadas, 2006) in a more general, larger context.

Surprisingly, we only detected two non-native species of northern France, both plant pests (Drake, 2009). The invasive ladybird H. axyridis was introduced in France in the middle 1990s and is now widely established (Brown et al., 2008). By competing with native ladybirds, H. axyridis seriously impacted the arthropod communities (Brown et al., 2008) and plants. It was the second highest abundant beetle species after the native ladybird C. septempunctata. The rosemary beetle C. aenea is native to southern France and is currently spreading north. This species is a pest of the Lamiaceae plant family (Drake, 2009).

4.4. Limitations

In this study, the substrate depth and the green roof age clearly correlated with the GR type and were not directly studied. We did not sample the biodiversity of substrates that, except for Collombolans (Schrader and Boning, 2006), are poorly known. Actually, our sampling method most likely underestimated the diversity of some nocturnal and/or litter dwelling and small (less than 2 mm) groups, such as rove beetles (family Staphylinidae) and money spiders (family Linyphiidae). These taxa are highly abundant in other urban green spaces (Vergnes et al., 2012) and some intensive green roofs (MacVor and Lundholm, 2011a) but were rare or absent in our study. Proper studies on the biodiversity of the substrate and the link between biodiversity and their functions are needed, e.g., to better assess the carbon sequestration potential of the different GR types (Getter et al., 2009). Our sampling method is a comparative approach and not an exhaustive inventory. Although our total abundance is lower than in other studies conducted on a limited number of sites, we performed a more extensive sampling. We used a comparative approach with a high number of sites and a high taxonomic resolution (individuals identified to species). Our method suffers from some limitations but retains several advantages. For example, the taxonomic precision allowed us to differentiate common species from xeric ones, which are often extremely morphologically close.

4.5. Applications of green roofs ecological design

Arthropods are rarely a priority in conservation actions or ecological studies (McIntyre, 2000; Hunter and Hunter, 2008). This rarity may be attributable to the recognition of moth and butterfly dwellers and even some ecologists (Kim, 1993). However, arthropods are a major component of ecosystems that span wild land to town centers (Wilson, 1987) and provide numerous ecosystem services, some of which exhibit a high economic value (Lossy and Vaughan, 2006). We demonstrated that maximizing the structural complexity of vegetation is the best way to enhance arthropod diversity. This positive effect could be enhanced by the creation of other habitats such as ponds, sand areas, rocks and dead wood (see Brenneisen, 2006 in Switzerland and Gedge, 2010 in England). A roofs are difficult to develop over pre-existing buildings due to the extra weight of the more complex vegetation and the necessary substrate depth. Architects and urban planners must focus on such complex green roofs on new buildings to develop urban biodiversity; when green roofs are included in the first steps of the building projects, the extra cost is minimized (<5% of the initial cost; Vanderpooten E., pers. com.). The H roofs could offer a compromise, as they can shelter only slightly less-rich communities in a lightweight structure that can be more easily implemented on a large range of existing roofs.

Sedums, in association with other more structured species, are an important component of the ecological design of green roofs, as
they can improve neighboring plant performance during a water deficit (Butler and Orians, 2011) and can be applied in numerous different situations. The use of native plant species is recommended and herbaceous species such as graminoids are sometimes more adapted to certain conditions than shrubs (MacIvor and Lundholm, 2011b). Overall, ecologists engineers must be included in the initial steps of these green building projects to adapt them to ecological issues.

5. Conclusion

We demonstrated the importance of the green roof type for arthropod communities and the presence of rare species in these habitat analogs. However, whether green roofs can function as ecosystems is still unclear. The mechanisms that explain the presence of xeric species from natural habitats that are generally located far from cities remain unknown. More generally, how landscapes foster green roof biodiversity needs further analysis. Proper studies on the colonization of organisms and the role of green walls in facilitating the access to green roofs by poor dispersers are also needed.

Biodiversity is only one of many needs of urban dwellers (Dearborn and Kark, 2010). Green roofs could provide many of these needs, justifying their additional cost (Carter and Keeler, 2008). Even the most basic need, food production, may be met with urban agriculture on rooftops (Whittinghill and Rowe, 2012). Nevertheless, biodiversity correlates with structural complexity and acts in synergy with other services rendered by “extensive” or “intensive” greening (Kosareo and Ries, 2007).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jecoleng.2013.04.029.

References


