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Micro-scale ecosystem differentiation and pollination network of the extensive green roof of the Terra Research Center

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MICRO-SCALE ECOSYSTEM DIFFERENTIATION AND POLLINATION NETWORK OF THE EXTENSIVE GREEN ROOF OF THE TERRA RESEARCH CENTER.

DELRUELLE ANNA

TRAVAIL DE FIN D'ÉTUDES PRÉSENTÉ EN VUE DE L'OBTENTION DU DIPLÔME DE MASTER BIOINGÉNIEUR EN GESTION DES FORÊTS ET DES ESPACES NATURELS.

ANNÉE ACADÉMIQUE 2019-2020

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Abstract

Green roofs are often praised for their contribution to supporting biodiversity. However, their ecological performance depends on their design and environmental conditions. This work addresses various ecological components of the roof of the TERRA building, three years after its installation. It focuses on two themes.

The first one addresses the differentiation of the ecosystem over time according to the depth of the substrate and the amount of sunlight received. Functional and taxonomic approaches revealed that the interannual variation in the plant communities of the roof was greater than the variations caused by substrate depth and sunlight. Over time, the communities evolved towards a more competitive and less stress-tolerant strategy. The analysis of the LHS traits suggested a community response to climatic events, particularly to the drought of spring 2020. After three years, a slight differentiation of substrates according to micro-environmental conditions was observed but was not the origin of the differentiation of plant communities.

The second theme focuses on the plant-pollinator network of the roof. The results show a low species diversity of pollinators, including only generalist pollinators. The evolution of insect captures and of the presence of flowering species within the quadrats suggests that greater plant abundance and diversity are needed to ensure the continuous delivery of floral resources to pollinators.

These two themes provide knowledge about the actual performances of the roof of the TERRA building and suggest the need for further research on the long-term resilience of green roof plant communities.

Résumé

Les toitures vertes sont souvent plébiscitées pour leur contribution au soutien de la biodiversité. Cependant, leurs performances écologiques dépendent de leur design et de leurs conditions environnementales. Ce travail aborde diverses composantes écologiques de la toiture du bâtiment TERRA, trois ans après son installation. Il s'articule autour de deux axes.

Le premier concerne la différenciation de l'écosystème au cours du temps en fonction de la profondeur du substrat et de l'ensoleillement reçu. Les approches fonctionnelles et taxonomiques ont révélé que la variation interannuelle des communautés végétales de la toiture avait été plus forte que les variations dues à la profondeur de substrat et a l'ensoleillement. Au cours du temps, les communautés ont évolué vers une stratégie plus compétitrice et moins stress-tolérante. L'analyse des traits LHS suggère une réponse des communautés aux événements climatiques, en particulier à la sécheresse du printemps 2020. Après trois ans, une légère différenciation des substrats en fonction des conditions micro-environnementales a été observé mais elle n'est pas à l'origine de la différenciation des communautés végétales.

Le second axe concerne le réseau de pollinisateurs de la toiture. Les résultats montrent une faible diversité d'espèces de pollinisateurs, comprenant uniquement des généralistes. L'évolution des captures d'insectes et de la présence des espèces en fleurs au sein des quadrats suggère qu'une plus grande abondance florale et une plus grande diversité végétale sont nécessaires pour assurer la délivrance continue de ressources florales aux pollinisateurs.

Ces deux axes apportent des connaissances quant aux performances effectives de la toiture du bâtiment TERRA et suggèrent la nécessité de poursuivre les recherches sur la résilience à long terme des communautés végétales sur les toitures vertes.

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General introduction

The purpose of this document is to explore various components of green roofs related to biodiversity support. It is composed of two distinct parts. The first one is related to micro-scale ecosystem differentiation on the extensive green roof of the TERRA building, located in Gembloux. It contains a scientific paper entitled: “Ecosystem differentiation at the micro-environmental scale on extensive green roofs” and its foreword. The later aims to broaden and better explain the concepts used in the introduction of the scientific paper. The second part is about the pollination network at the roof scale of the same building. It also contains a scientific paper entitled: “Plant-pollinator network in real extensive green roof conditions” and its foreword. This document ends with a concluding paragraph on our work, its perspectives and the connections that can be made with the study conducted by Séverine Degailler, who also studied plant-pollinator interactions on the TERRA building (Degailler, Mahy and Francis, 2020).

Part 1

Foreword: Ecosystem differentiation at the micro-environmental scale on extensive green roofs.

1) Introduction

The world is currently facing great structural changes. One of the major shifts is biodiversity loss. Urban development as well as suburban sprawl trends do constitute a serious source of pressure on natural ecosystems. As population growth will keep raising in the next decades, anthropogenic habitats need to be adapted in order to cope with biodiversity decline (McGranahan and Marcotullio, 2005).

Green roofs are "nature based solutions", i.e. actions inspired by, supported by or copied from nature (European Commission, 2015). They aim to respond to current challenges through the diversity of ecosystem services they are meant to provide, including biodiversity enhancement. Their service attainment varies according to the substrate chosen, its thickness, the vegetation cover, the proportion of impermeability of the surrounding environment, etc. (Lundholm *et al.*, 2010; Oberndorfer *et al.*, 2007; Vaz Monteiro *et al.*, 2017).

Green roofs may be integrated into green infrastructures which are networks of landscape continuities within the urban matrix allowing connectivity between small ecosystem patches (European Commission and Directorate-General for the Environment, 2014). Thus, they may densify the urban network of biodiversity refuges and can serve as a "stepping zone" for many taxonomic groups.

Insofar as green roofs are envisaged as a real solution to support biodiversity, it is essential to study their performance as a biodiversity refuge for both animal and plant communities. This assessment can only be achieved by a strong comprehension of the factors influencing ecosystem differentiation. Green roofs evolve over time, which can result in a divergence of the substrate composition and of the plant cover, including mosses (Brown and Lundholm, 2015; Buffam and Mitchell, 2015). Thus, assessment needs to be conducted over several growing seasons in order to understand the dynamics driving ecosystem differentiation.

2) Green roof types and definition

Green roofs are obtained by covering a conventional roof with a growing medium (Young, Chase and Huddleston, 2001) complemented by other layers (fig.1), such as draining, filtering or insulating layers (Peck and Kuhn, no date). The latter prevent water stagnation and root damage to the infrastructure (Vandooren, 2006).

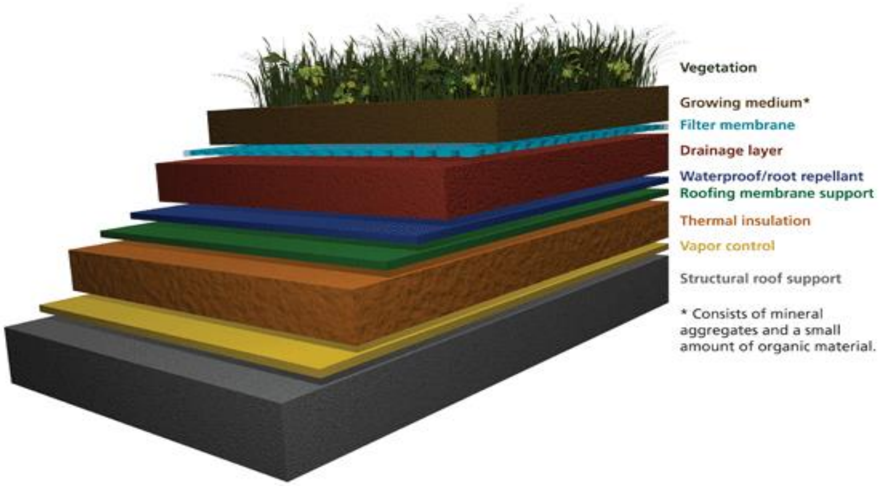


Figure 1: Cross section of green roofing layers. Illustration: Blank Space LLC. National Park services, U.S. Department of the Interior

Green roofs are generally classified according to their substrate depth. Extensive roofs have a shallow substrate (2 to 20 cm), while intensive roofs have a deeper one (more than 20 cm) (Nagase and Dunnett, 2010). The number of depth classes varies, with some authors distinguishing an intermediate category: semi-extensive roofs (Peck *et al.*, 1999; Vandooren, 2006). The boundaries between roof types vary among papers and are simply a matter of definition, as the full range of depths is possible.

Intensive roofs accommodate the greatest diversity of plants, since various depths can be exploited by the different root ranges. A wider number of species are therefore able to adapt to substrate depth (Dunnett, Nagase and Hallam, 2008; Oberndorfer *et al.*, 2007; Rowe, Getter and Durhman, 2012). Their greater biodiversity potential also extends to arthropod communities, which are more likely to find shelter or food resources within a wider plant diversity. In addition, the greater density and plant diversity of intensive roofs would allow for the improvement of some regulating services (Getter and Rowe, 2006; Lundholm *et al.*, 2010). Despite these advantages, intensive roofs are rare, due to the additional load on the infrastructure and the greater need for maintenance (Nagase and Dunnett, 2010; Oberndorfer *et al.*, 2007; Peck and Kuhn, no date; Vandooren, 2006).

A second classification consists of describing the plant strata covering the roof rather than the substrates. Thus, a distinction is made between muscinal, herbaceous or arbustive roofs. The last two categories are characterized respectively by the presence of at least 20% herbaceous or arbustive plants (Madre *et al.*, 2013). The author argues that this type of classification better reflects the diversity of plant structures and its potential for hosting microfauna.

3) Habitat analogues

Extensive roofs can be described through their “habitat template”. This term refers to the physico-chemical parameters distinguishing habitats (Southwood, 1977). This concept allows to identify different habitats combining the same structural parameters (analogous habitats). Thus, although urban environments are "novel ecosystems", i.e., ecosystems whose species assemblage and configuration has never been observed before (Hobbs *et al.*, 2006), they may resemble certain natural ecosystems (Lundholm, 2006).

Extensive green roofs are characterized by particularly stressful conditions. Indeed, their shallow substrate, placed on an impermeable surface, can lead to both drought and flooding during the same growing season (Lundholm, 2006). However, drought conditions are generally the most limiting. Indeed, a porous substrate is usually chosen in order to avoid the structure to be overloaded (Oberndorfer *et al.*, 2007). In addition, the height of the roof can expose the plants to wind and important amounts of sunlight, the latter causing significant variations in the temperature of the substrate (Nagase and Dunnett, 2010; Catalano, Guarino and Brenneisen, 2013). Finally, the substrate is generally relatively poor.

These stressful conditions are similar to those in dry or rocky, first succession environments, where the substrate is shallow and low in nutrients. Species found in cities are of varied origins but are often found in hostile habitats. Many species in these dry environments have adaptations enabling them to avoid drought (dormancy) or to resist it. Extensive roofing conditions keep the succession in the primary stage permanently (Lundholm, 2006).

Extensive roofs and some natural environments such as xeric to meso-xeric calcicolous grasslands have a similar habitat template and can be qualified as analogous (Lundholm, 2006). Calcicolous grasslands are one of the most diverse ecosystem in temperate western Europe and are threatened by land use change (Piqueray and Mahy, 2010). It would therefore be interesting to evaluate the ability of their flora to develop on green roofs and create analog communities. It would add some ecological value to extensive roofs by reinforcing green infrastructures.

4) Effects of environmental variables on plant communities

Variables such as the nature and depth of the substrate, temperature, precipitation regime, luminosity, size and nature of the micro-habitats, specific diversity and interspecific interaction modify the dynamics of establishment and maintenance of plant communities (Catalano, Guarino and Brenneisen, 2013). Although there is a common set of conditions for extensive roofs, local and temporal variations can be significant due to the diversity of factors influencing these dynamics.

On green roofs, substrate depth is the most constraining factor influencing the development of plant communities since it conditions the water reserve and the stability of the substrate temperature (Brown and Lundholm, 2015). Thus, shallower substrates preferentially support mosses and sedums (Nagase and Dunnett, 2010) while grasses and forbs grow on deeper substrates (Brown and Lundholm, 2015; Köhler, no date; Nagase and Dunnett, 2010). Extensive roofs also qualify for a higher survival rate of vegetation as they allow a greater water retention (Brown and Lundholm, 2015; Madre *et al.*, 2014; Nagase and Dunnett, 2010).

A second constraining factor is roof exposure (Brown and Lundholm, 2015) since it influences the evaporation of water from the substrate and evapotranspiration by plants. Thus, the most drought-resistant plants such as succulents and bryophytes can resist to a greater sun exposure.

These two factors being the most limiting ones for plant growth and survival, it is essential to assess their influence on the targeted flora in the local context of the roof.

Other factors such as roof height or maintenance level also influence the functional diversity of the roof, since they determine other factors such as exposure to wind or the level of disturbance of the community (MacIvor, 2016; Madre *et al.*, 2014). However, these factors tend to have a smaller influence than substrate depth and sun exposure.

5) Temporal evolution of plant communities

Green roofs evolve over time (Madre *et al.*, 2014; Brown and Lundholm, 2015; Piana and Carlisle, 2014). The age of the roof is therefore a determining factor in the composition of the plant community. For example, a set of roofs installed in Wollishofen in 1914 is home to 175 species, including red-listed orchids. The success of this roof, which is close to the surrounding natural ecosystems, is the result of the use of the local soil as a substrate as well as its age, which has allowed local species to colonize and adapt to the local dynamics of the area (Brenneisen, 2006; Catalano, Guarino and Brenneisen, 2013).

Temporal evolution of communities also is influenced by the order of settlement of the species. Indeed, pioneer species may have a competing or facilitating effect on slower-growing species (McCallum *et al.*, 2018; Young, Chase and Huddleston, 2001). For instance, mosses have been found to have both effects on vascular plant growth. They buffer harsh environmental conditions (Heim, Lundholm and Philip, 2014) and facilitate trap seed but may also form a dense layer preventing seeds from emerging the moss canopy (Drake *et al.*, 2018). The growth speed of plants thus influences their success or failure as well as the settlement of slower growing species.

Dispersal syndrome and seed mass are important factors too, as they determine plant dispersion, seed survival and seedling number (Westoby, 1998).

Competition of local colonizing species as well as seed density therefore play decisive roles for roof communities (Brenneisen, 2006; McCallum *et al.*, 2018). Thus, a decrease in the number of planted species coupled with an increase in colonizing species can be observed over time (Brown and Lundholm, 2015). Although rooftop communities stabilize over time, they are sensitive to climatic events and can therefore be subject to interannual variations (Piana and Carlisle, 2014). Drier years would therefore be characterized by lower species diversity (Brown and Lundholm, 2015).

The diversity of plant traits and the configuration of the assembly also influence the survival and performance of the roof. This is explained by a better use of the various ecological niches and their resources (Nagase and Dunnett, 2010).

Temporal evolution can be explained by functional traits of the planted and colonizing species. The "response-effect trait framework" hypothesis suggests that plant communities are determined by the response of species traits to the environment, but also that ecosystem functioning is influenced by the traits that make up the community. There is therefore a reciprocal influence of traits on the environment, which implies a time of stabilization of communities and the environment (Zirbel *et al.*, 2017).

6) Temporal evolution of green roof's substrates

Substrate is a crucial characteristic of green roofs. It conditions nutrient availability and water retention and by implication, the plant composition of the roof. Studying how substrates evolve over time in relation to plant communities is thus very important to understand ecosystem differentiation. Substrate depth and composition are the main factors influencing soil moisture on green roofs. The presence of fine particles (clay and silts) improves the water retention of green roofs (Chenot *et al.*, 2017). These factors are known to be changing over time as substrate may be subject to settlement, leaching (Buffam and Mitchell, 2015) or degradation (De-Ville *et al.*, 2017; Getter and Rowe, 2006). In some studies, an increase in porosity, fine particles and organic matter content has been shown (Getter and Rowe, 2006; De-Ville *et al.*, 2017, p.). These structural changes may increase water holding capacity, depending on the initial system's properties (De-Ville *et al.*, 2017; Getter and Rowe, 2006).

In contrast, a study showed a loss of organic matter and an early ageing of the substrate structure leading to reduction of the water holding capacity (Bouzouidja *et al.*, 2018). Several studies show that leaching from green roofs may be a source of eutrophication (Buffam and Mitchell, 2015) or metal pollution (Speak *et al.*, 2014). High leaching of Phosphorus and Nitrogen often result from rich substrates combined with a vegetation that is adapted to low-nutrient environments (Buffam and Mitchell, 2015).

These contrasting results originate from the differences in the initial substrate, in their treatments and their plant cover (Buffam and Mitchell, 2015). Plant composition also influences nutrient and water retention, acting more or less efficiently on carbon storage (Whittinghill *et al.*, 2014) and on water runoff (McCallum *et al.*, 2018).

To date, substrate evolution has not been studied in relation with its exposure or depth. As both factors have an influence on plant communities, which themselves act on soil structure, further research including these three components need to be carried out.

7) Functional traits approach

Plants possess morpho-physiophenological attributes that affect their individual performance in terms of growth, survival and reproduction. These attributes are called functional traits. The presence of certain "response traits" enables vegetation to overcome the barriers constituted by environmental variables in a given situation (Violle *et al.*, 2007).

Thus, plant communities have a set of traits that allow them to persist in their environment (Lavorel *et al.*, 2007; Zirbel *et al.*, 2017). Sets of traits can be grouped into various adaptative strategies based on the components of individual performance. As compared to taxonomic analysis, the study of plant communities based on their functional traits provides a greater understanding of the processes underlying their evolution and response to environmental factors. It therefore allows to compare different pools of species.

8) CSR strategies

The C-S-R model (Grime, 1974, 1977, 2001) assigns to each species a degree of investment in stress resistance (S), ruderality (R) and competition strategies (C). These components are represented in a triangular system. The position of the species within this system gives a value for the relative share invested in each of these components (Hodgson *et al.*, 1999)

Two factors define CSR strategies: stress intensity and disturbance intensity. Stresses are environmental factors that limit plant growth or reproduction, such as water or nutrient shortage. Disturbances represent all sources of destruction or deterioration of the biomass of the flora. For instance, herbivory, extreme climatic events, trampling or exploitation are considered as disturbances.

Three ecological behaviours are possible. If the two factors are of low intensity, competitiveness will be favoured. When only stress is high, resistance is adopted. Ruderality develops if the stress is moderate but the disturbances increase. When the intensity of both factors is too high, survival is simply impossible (Hodgson *et al.*, 1999).

These strategies are characterized by the presence of various traits within the communities. For example, competitors mainly invest their resources in growth and lateral spreading, which allows them better access to resources, especially light. Ruderal species allocate their energy to reproduction, allowing for rapid and abundant offspring between disturbances (Grime, 1977). Stress resistant species maximize nutrient and water storage within their tissues (Lundholm, 2006). This storage can be achieved by accumulation or by limiting losses. For example, the CAM photosynthesis of sedums enables them to limit water loss through evapotranspiration and contributes to their particular resistance to water stress (Nagase and Dunnett, 2010).

This model takes into consideration the effects of climate or plant exploitation. It therefore improves the r/K model, which distinguishes only the most extreme strategies. It gives a more complete vision of the system’s dynamics. For instance, it is a relevant framework in land use studies where the C-axis represents abandonment, the S-axis corresponds to eutrophication level and the R-axis to the disturbance rates (Hodgson *et al.*, 1999).

This model provides a typology based on a quantitative methodology and as such, allows comparisons between multiple species. It has been recognized as a promising tool for comparative ecology in first succession environments (Caccianiga *et al.*, 2006). It is based on a wide range of traits and is therefore very integrative (Hodgson *et al.*, 1999). However, its interpretation in terms of specific traits involved is very difficult. The contribution of individual traits in the general strategy of a species remains unclear. For this reason, a complementary approach based on individual traits may be useful.

9) LHS model

The Leaf-height-seed (LHS) approach is a three dimensional model based on three uncorrelated variables: specific leaf area (SLA), canopy height and seed mass (Westoby, 1998). These axes were defined on the strength of their explanatory power of some related traits. It was demonstrated that even some underground traits were explained by the LHS system. For instance, fine roots and leaf nitrogen concentration both are positively correlated to SLA and seed mass is negatively correlated with specific root length (Laughlin *et al.*, 2010).

This model allows its user to define plant strategies without losing its perspective on the traits involved. It was created to simplify the complexity of assessing plant strategies. The slightly lower explanatory power of LHS as compared to CSR system is counterbalanced by two great advantages. First, its modeling is facilitated by its limited number of traits that are easily measurable. It is therefore easier to assess communities whose species are not comprised in the pre-established CSR databases. Second, it allows comparisons on a worldwide scale. This is not the case of the C-S-R model whose correlation between traits and strategies were standardized only on British flora (Westoby, 1998).

CSR and LHS models, while showing different representations, present a lot of similarities. The SLA axis is related to the responsiveness to opportunities for rapid growth. This corresponds to the C-S axis of the CSR system. The R axis of Grime's model corresponds to ruderality while in LHS, height and seed mass represent two different components of resistance to disturbance.

Even though the two models tend to represent the same ecological processes on their axes, they sometimes show different results in comparing plant strategies (Moog, Kahmen and Poschlod, 2005). LHS system, while providing a more targeted approach sometimes does not include all the explanatory components of a community strategy. For this reason, both models have been considered as complementary in this paper.

Experimental contribution: Ecosystem differentiation at the micro-environmental scale on extensive green roofs.

1) Abstract

Extensive green roofs may contribute to biodiversity support. However, the evolution of their plant communities according to micro-environmental factors remains poorly understood. Thirty-six quadrats of an extensive roof were monitored over three years, in Southern Belgium. Coverage by species was surveyed for three classes of sun exposure (low, medium, high) and two classes of substrate depth (6 and 11cm). Moss cover surveys and an analysis of substrate samples were added in the third year of the experiment. After three years, the taxonomic and functional approaches showed that interannual variation had a greater effect than exposure and depth on plant communities. The influence of substrate depth and sun exposure on plant communities decreased over time. The CSR model revealed a temporal evolution of the mean community strategy, resulting in an increase in competition and a decrease of stress-tolerance. The LHS model showed interannual and micro-environmental variations at the community level, except for seed mass. Exposure effected the SLA in the deepest quadrats, leading to a higher SLA in low exposure quadrats. Canopy height was significantly higher in the deepest quadrats. There was a significant effect of both exposure and depth on moss cover, leading to a higher moss colonization in low exposure and in 11 cm quadrats. Micro-environmental factors significantly influenced organic carbon content, silt percentage and water pH. However, the substrate differences among modalities were negligible from an ecologic perspective and were shown not to be the cause of the taxonomic distinction among micro-environmental modalities (substrate depth and sun exposure). In this study, we show that green roof plant communities have not stabilized after three years. We suggest a longer-term research to better understand the effect of extreme climatic events on plant community resilience.

2) Introduction

In the context of biodiversity decline, green roofs can be integrated into urban green infrastructures designed to reinforce connectivity between small ecosystems patches within the urban matrix (European Commission and Directorate-General for the Environment, 2014). Green roofs may densify the urban network of biodiversity refuges, depending on their plant cover.

Green roofs may be described through their habitat template, i.e. the set of physico-chemical parameters distinguishing habitats (Southwood, 1977). The "habitat template" approach allows to identify analogous habitats, that can be defined as 'anthropogenic ecosystems able to support indigenous biodiversity due to their structural or functional resemblance to natural ecosystems, habitats, or microsites that may be present in the region, but not part of the historic ecosystem on a particular site' (Lundholm and Richardson, 2010). As urban and anthropogenic environments tend to expand around the world (Seto *et al.*, 2011), the ability of green roof ecosystems to behave as analogous habitats needs to be assessed. This requires a holistic approach considering the different components of the ecosystem: plant communities and abiotic conditions.

Extensive green roofs have a maximal substrate depth of 20 cm (Nagase and Dunnett, 2010). Their ability to accommodate plant species is limited as compared to intensive roofs with deeper substrate, where a wider root range can be exploited (Dunnett, Nagase and Hallam, 2008; Oberndorfer *et al.*, 2007; Rowe, Getter and Durhman, 2012). Drought conditions are generally the most limiting. A porous substrate is usually chosen in order to avoid the structure to be overloaded (Oberndorfer *et al.*, 2007). The height of the roof can also expose the plants to wind and important sunlight, the latter causing significant variations in the temperature of the substrate (Catalano, Guarino and Brenneisen, 2013; Nagase and Dunnett, 2010).

These limiting conditions are of interest to maintain the ecological succession at the primary stage permanently (Lundholm, 2006). Extensive roofs resemble dry or rocky, first succession environments, where the substrate is shallow and low in nutrients (Lundholm 2006). Their potential for biodiversity enhancement as analogous habitat is important. Extensive roofs and some natural environments such as xeric to meso-xeric grasslands have a similar habitat template (Lundholm, 2006). Dry grasslands are diverse ecosystems, which are of interest in urban environments. Extensive green roofs could possibly contribute to their development.

Environmental variables such as the nature and depth of the substrate, temperature, precipitation regime, luminosity, size and nature of the micro-habitats, specific diversity and interspecific interaction modify the dynamics of establishment and maintenance of plant communities (Catalano, Guarino and Brenneisen, 2013). Although there is a common set of conditions for extensive roofs, local and temporal variations can be significant due to the diversity of factors influencing these dynamics.

Temporal dynamics also play a key role in green roof community settlement. The evolution of communities during the first years after settlement therefore needs to be studied. Development of species may be impaired (Young, Chase and Huddleston, 2001) or facilitated (Brenneisen, 2006; McCallum *et al.*, 2018) by pioneer species. For instance, mosses have been found to have contrasting effects on vascular plant growth. They buffer harsh environmental conditions (Heim, Lundholm and Philip, 2014) and facilitate trap seed but may also form a dense layer preventing seeds from emerging the moss canopy (Drake *et al.*, 2018). The age of the roof is an important factor as local species may colonize the roof over years while planted species tend to decrease (Brown and Lundholm, 2015). Although rooftop communities stabilize over time, they are sensitive to climatic events and can therefore be subject to interannual variations (Piana and Carlisle, 2014).

Temporal evolutions can be explained by the "response-effect trait framework" hypothesis, that suggests a reciprocal influence of plant species traits on the environment, which implies a time of stabilization of plant communities and the environment (Zirbel *et al.*, 2017). An increased cover of vascular plants and mosses would improve water retention of the substrate (Anderson, Lambrinos and Schroll, 2010; Chenot *et al.*, 2017; McCallum *et al.*, 2018) and consequently leaching and degradation. Aging substrate may evolve differently depending on its initial chemical composition, on its maintenance, on its depth and on its plant composition (Buffam and Mitchell, 2015; Chenot *et al.*, 2017; McCallum *et al.*, 2018). To date, the influence of substrate depth and exposure on the composition of aging roofs remains unknown. Given the importance of soil composition in the resulting ecosystem, further research is needed.

The dynamics of green roofs depend on the species they host. Functional traits assessment constitutes an interesting approach to study species assemblages. It allows to identify functional patterns independently from the local pool of species. As compared to taxonomic analysis, it provides a better view of the processes that govern species succession. It can thus be extended to a wider set of species than those studied in a specific context (Woodward and Cramer, 1996).

The C-S-R model (Grime, 1974, 1977, 2001) relies on functional traits to group plant species into various adaptative strategies based on the components of individual performance. It
assigns to each species a degree of investment in stress resistance (S), ruderality (R) and competition strategies (C) (Hodgson *et al.*, 1999). This model provides a very integrative vision of plants strategies and a quantified evidence-based typology.

However, it does not provide an easy interpretable result in terms of specific traits and of how traits individually contribute to the community strategy. An analysis of specific traits can therefore be a complementary approach to study green roof communities.

The LHS model (Westoby, 1998) aims at simplifying plant strategies assessment. It is based on three uncorrelated functional traits: specific leaf area, canopy height and seed mass. These traits were chosen according to their explanatory power of other related traits. SLA is strongly related to leaf and fine roots nitrogen concentration (Laughlin *et al.*, 2010). Despite its lower explanatory power, LHS model facilitates calculation for species that are not comprised in CSR databases and allows worldwide comparisons. This is not the case of the C-S-R model whose correlation between traits and strategies were standardized only on British flora (Westoby, 1998).

In this study, we assess how sun exposure and substrate depth influenced ecosystem differentiation over time on an extensive green roof composed of dry grasslands species. Our specific questions are: 1) How do vascular plant communities differentiate according to sun exposure and substrate depth over three years, from a taxonomic and functional perspective? 2) Three years after the installation of the roof, does the substrate composition differ according to micro-environmental conditions?

3) Materials and methods

3.1) Study site

An extensive green roof, located in Gembloux, southern Belgium (50°33’48” N 4°41’52” E), was studied over three consecutive years (2018-2020). It lies on the roof of the TERRA building, at approximately 5,4 m high. The climate is a temperate oceanic climate (Cfb), according to Köppen climate classification (Belgian Federal Service, s. d.). The three years of the study were characterized by abnormal temperatures and precipitations for April, May and June as compared to the average climatic variables of the reference period (1981-2010), in Gembloux. An excess in temperature ranging from 0,5° to 3°C was recorded, except for May 2019, which presented a temperature deficit of 1,5°C (IRM, 2020a).

Precipitation rate was lower than the norm except for May and June 2019. April and May 2020 were particularly dry with respective precipitation rates of only 40 and 20% of the normal values (IRM, 2020b).

The roof is composed of 9 experimental plots, whose size varies from 14 m² to 57 m², sown in October 2017 (total: 254m²). Plots have a substrate depth of either 6 (5 plots) or 11 cm (5 plots) after settling. They are composed of "Zinco Extensive Green Roof Substrate©".

The plots are oriented East-West and the roof is surrounded by walls on three of its sides (North, East and South). The skylights installed between certain plots create a gradient of north-south exposure of the roof. Three classes of exposure corresponding to the maximum number of hours of sunshine per day were determined (Bernard, 2018): low exposure (3 to 6h), medium exposure (6 to 9 h) and high exposure (9 to 12h) (fig.2). The hand-seeded mix contains 29 native species selected according to their habitat: xeric to meso-xeric calcicolous grasslands. Of these species, five are Poaceae and three are native *Sedums* (Appendix 1).

3.2) Data Collection

Data were collected at the end of June 2018, 2019 and 2020. Sampling was carried out in 1 m² quadrats, placed in such a way as to capture all depth and sunshine modalities. Within the large plots, permanent quadrats were randomly installed. For each small plot, two quadrats were lined up in a systematic arrangement (fig 2).

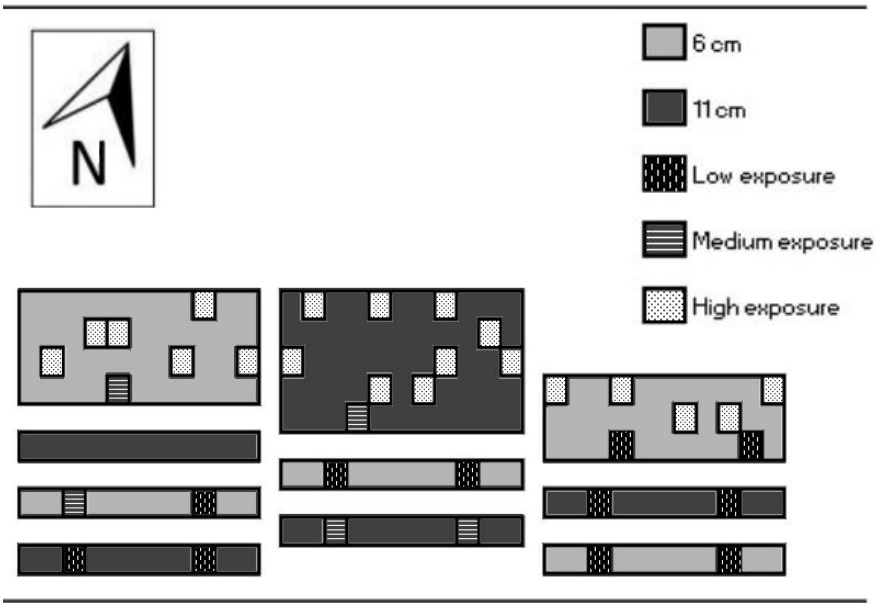


Figure 1: Sun exposure and depth of the quadrats within the extensive plots of the TERRA building (Gembloux, Belgium).

Vascular plants and mosses abundance were quantified using the point quadrat method. A perforated Plexiglas plate with 100 holes spaced 10 cm apart was used. A needle was lowered into each hole and the number of contacts with every species was recorded. Contacts were recorded for each species of vascular plant. Mosses were only recorded in 2020. They were not identified to species level and were consequently aggregated. The relative coverage was then calculated using Barbour's formula:

$$Species\ A\ relative\ cover = \frac{Number\ of\ needles\ touching\ A\ at\ least\ once}{Total\ number\ of\ needles} \times 100$$

A composite sample of substrate was taken in each quadrat in June 2020 in order to determine structure and composition. Soil samples were analyzed through physical analyses to identify the texture (sand, silt and clay percentage) and water pH (pH). Total organic C (g/Kg) was determined following the Springer–Klee method (Springer and Klee, 1954). Humus percentage was calculated using conversion factor of 2 (Pribyl, 2010). Total nitrogen content (%N) was estimated by modified Kjeldahl method (Nelson and Sommers, 1982). C/N ratio (C/N) was deducted from the division of organic carbon by %N. CaCo3 content (CaCo3) was estimated by modified Dourniaud-Galet method (Guilloux-Benatier, Duteau and Seguin, 1978). P content (mg/100g) was determined after an extraction by 1 N of CH3COONHEDTA (pH 4.65) for 30 min (ratio soil:solution of 1:5)(Lakanen and Erviö, 1971). Potassium (K) was extracted following the same method (Lakanen and Erviö, 1971)and was dosed by atomic absorption spectrophotometry (mg/100g).

3.3) Analyses

Data analysis was performed using R 3.6.3 (R Core Team, 2019) and Microsoft Excel 2010 (Microsoft Corporation, 2010). Normality and heteroscedasticity were tested retrospectively ("plot" command, multcomp (Hothorn, Bretz and Peter, 2020), on model residuals. Graphs of the analysis of the residues are set out in the appendices section.

3.3.1) Plant communities' analysis

To characterize variation in plant composition in quadrats, Principal Coordinates Analyses (PCoA) based on the Bray-Curtis dissimilarity matrix were performed for the aggregation of the three years and for the years 2018 and 2019. This analysis was used to characterize the floristic composition patterns every year and their evolution over time. Species whose correlation to principal components was greater than 0.35 in absolute value were plotted in a correlation circle.

3.3.2) Analysis of CSR indices in relation to environmental factors

The mean coordinates of the C, S and R components were calculated for each plant community in each quadrat for the three years, based on the relative abundance of the species within the quadrat. The components of each species were found in Hodgson's Databases (1999), except for *Dianthus carthusianorum* L. (Kingsbury, 2008) and *Bromus erectus* Huds. (Pierce *et al.*, 2013).

The C-S-R components of each year were represented in a single triangular diagram (Compositions package) (van den Boogaart, Tolosana-Delgado and Matevz, 2020).

Mean C, S and R percentages at the plant community level were compared among sun exposure classes, susbtrate depths and years with a linear mixed-effects model with repeated measures, the repeated factor being the identity of the quadrat ("lmer " command, lme4 (Bates *et al.*, 2020) and "Anova", car (Fox *et al.*, 2020)). Tuckey post-hoc tests were performed when necessary ("emmeans", emmeans (Lenth, 2020)).

3.3.3) LHS assessment in relation to environmental factors

For each annual survey of species cover, average community LHS traits of each quadrat were calculated using the formula:

$$Average\ community\ trait = \sum(p_i * trait_i),$$

p_i being the relative cover of the species i and $trait_i$ being the value for the trait for species i.

SLA, seed mass and height canopy were obtained from the LEDA traitbase database (Kleyer *et al.*, 2008). Traits were calculated as the average of the available data for the considered species. Only data from France, Germany, United Kingdom and the Netherlands were included. For seed mass, only data based on germinules was included.

Mean plant community traits were compared among sun exposure classes, susbtrate depths and years with a linear mixed-effects model with repeated measures, the repeated factor being the identity of the quadrat ("lmer " command, lme4 (Bates *et al.*, 2020) and "Anova", car (Fox *et al.*, 2020)). Tuckey post-hoc tests were performed when necessary ("emmeans", emmeans (Lenth, 2020)).

3.3.4) Moss cover

Mean moss cover in 2020 was compared among sun exposure classes and substrate depths with a two-way ANOVA. Tuckey post-hoc tests were used to test for differences among covers for sun exposure ('glht' command, multcomp).

3.3.5) Soil structure and composition

A principal component analysis (PCA) was performed on soil data of 2020 ("princomp" command, stats). Mean values of uncorrelated variables were then compared with a two-way anova among sun exposure classes and substrate depths. Tuckey post-hoc tests were used when a significant difference between exposure classes was observed. A constrained analysis of principal coordinates (CAP) based on the Bray-Curtis dissimilarity matrix was also performed to link soil composition to plant communities. The model, the axes and soil variables were tested with permutation tests for the significance of constraints ('anova' command, vegan (Oksanen, 2017)).

4) Results

4.1) Plant communities' analysis

The first two axis of the aggragated PCoA (fig.2a) based on quadrat plant composition over the three years observation (2017-2020) explained 27% of plant composition variation (PCoA1= 15,0%, PCoA2= 12,4%). The third axis was not considered as its contribution to the explanatory power was small. The aggregated PCoA (fig.2a) shows an effect of interannual variation on the taxonomic composition. This effect is greater than the effect of depth and exposure on plant composition.

Anthoxanthum odoratum L., *B. erectus, Anthyllis vulneraria* L., *Briza media* L., *Echium vulgare* L. and *Rumex acetosella* L. are the most negatively correlated with the first axis of the aggregated PCoA (fig.3b). These species are those who distinguish the most the quadrats of 2019 from the two other years. The most positively correlated species to the second axis were *Koeleria Macrantha* (Ledeb.) Schult. and *Medicago lupulina* L., which distinguish quadrats from 2018 from the two other years.

When years are considered separately, a distinction among micro-scale modalities can be observed. In 2018, the PCoA explained 41% of plant composition variation (PCoA 1= 25,0%, PcoA 2= 15,6%). Quadrats were distributed according to their exposure and depth along the first axis of the PCoA (fig. 3a). High exposure quadrats were mainly distributed in negative coordinates of the first axis. The quadrats with the deepest modality (11 cm) were mainly represented in positive coordinates of the first axis. The second axis showed an arch effect, which reflects an unrepresented gradient in its dimension. In 2020, the PCoA explained 31% of plant composition variation (PCoA 1= 17,8%, PcoA 2= 12,9%). Highly exposed quadrats were mainly distributed in the positive coordinates of the first axis. No clear pattern was observed for depths modalities among quadrats (fig. 3b).

Dominance dynamics vary among years (fig.4 and fig.5). The first year was characterized by an abundant cover of *K. Macrantha,* which dropped afterwards. *A. odoratum, B. erectus, A. vulneraria, B. media* and *E. vulgare* were dominating the plant composition of the quadrats in both 2019 and 2020.

However, their cover was lower in 2020. The latter was characterized by a higher cover of the three *Sedum spp.* Total plant cover was of 25,4% in 2018, of 81% in 2019 and 36,8 % in 2020.

The composition also varied with the disappearance of sown species and invasion unsown species (fig.5). Some species were successful in the first year but disappeared over time (*Poa Pratensis* L., *Tragopogon pratensis* L. and *Scabiosa Columbaria* L.). Some species were exclusively present in the second year (*Primula veris, R. acetosella* L., *Centaurea scabiosa* L. *and Sanguisorba minor* Scop.*)*. Over time, unsown species colonized the roof (*Trifolium pretense* L.*, Trifolium arvense* L., Sonchus Oleraceus L., *Vicia sativa* L.).

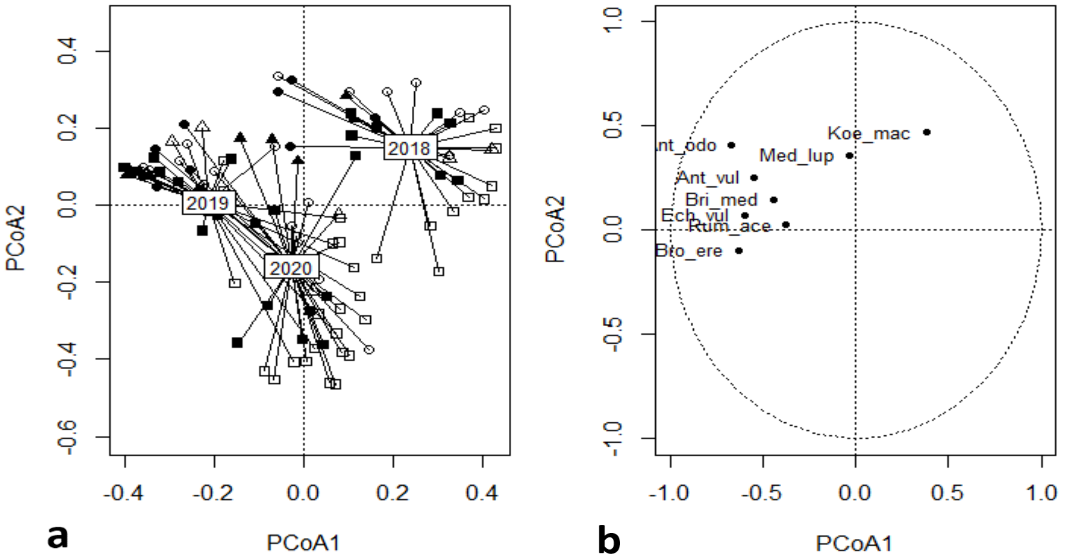


Figure 2: Principal coordinates analysis of plant communities of the extensive green roof plots of the TERRA building (Gembloux). a) PCoA labelled per year (Dim1=15,02%; Dim2= 12,37%). Symbols represent exposure (circle= low, triangle= medium and square= high) and depth (white= 6cm, black= 11 cm. b) Correlation circle of species with a with a higher correlation than 0,35 in absolute value with one the two first axes of the PCoA.

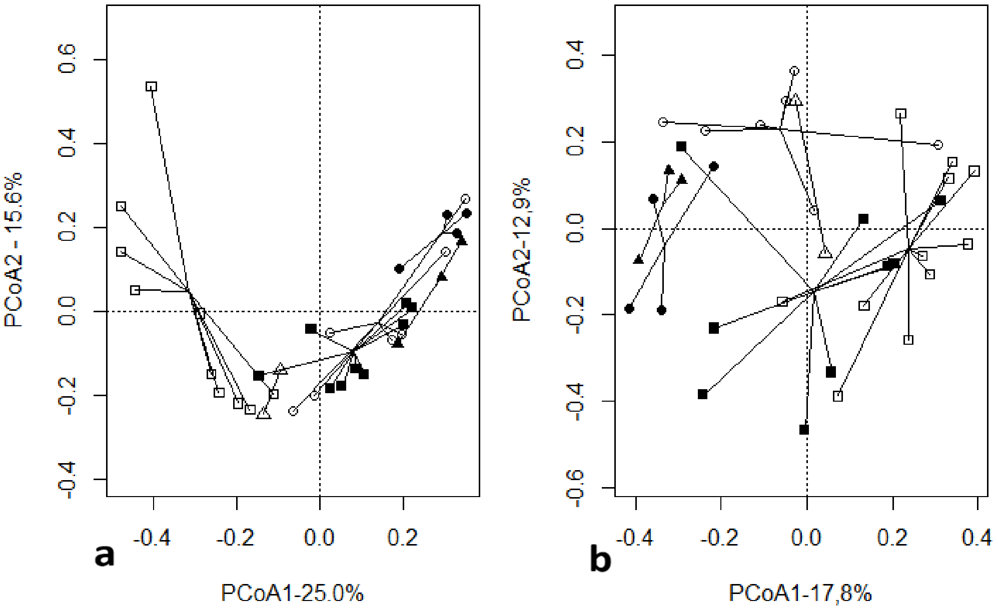


Figure 3: Principal coordinates analysis of plant communities of extensive green roof plots, located on the TERRA building (Gembloux). Symbols represent exposure (circle= low, triangle =medium and square=high) and depth (white= 6cm, black= 11 cm. Ordispiders are pooled by combination of substrate depth and sun exposure. a) 2018 (PCoA1=25,0%; PCoA2= 15,6%). B) 2019 (PCo1=17,8%; PCoA2= 12,9%).

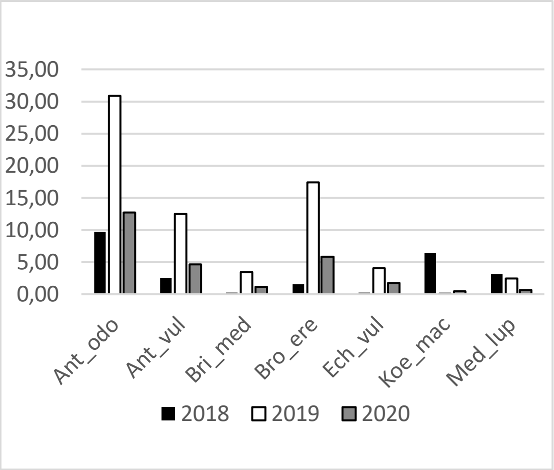


Figure 4: Evolution of the plant cover of the dominant species of the extensive green roof of the TERRA building from 2018 to 2019

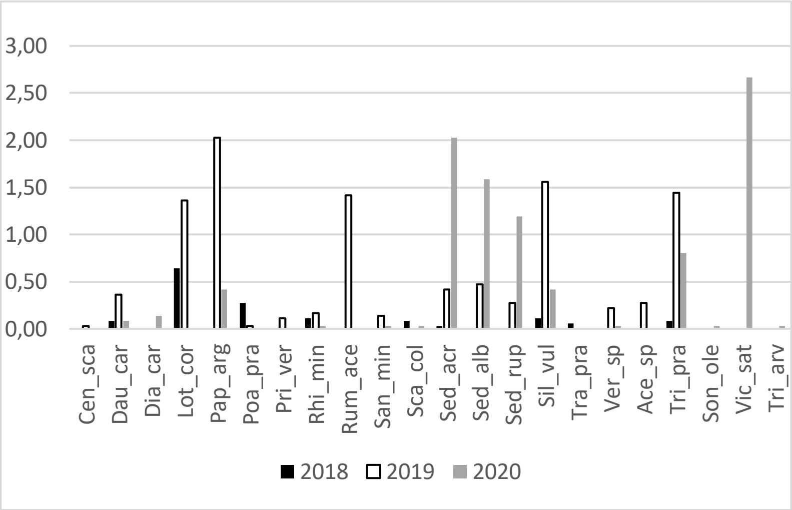


Figure 5: Evolution of the plant cover of the minor species of the extensive green roof of the TERRA building from 2018 to 2019

4.2) Analysis of CSR indices in relation to environmental factors

Linear mixed-effects model with repeated measures revealed a significant effect of the year for %C (p < 0,001) and %S (p < 0,001) but not %R (p > 0,05, fig.7). Mean %C in 2018 (global mean ± standard deviation= 0,14% ± 0,3%) was significantly lower than both 2019 (0,22% ± 0,5%) and in 2020 (0,23% ± 0,1%). Mean %S was significantly higher in 2018 (0,55% ± 0,01%) than in 2019 (0,40% ± 0,05%) and 2020 (0,43% ± 0,15%). It showed no significant effect of substrate depth or sun exposure on %C, %S or %R (p > 0,05).

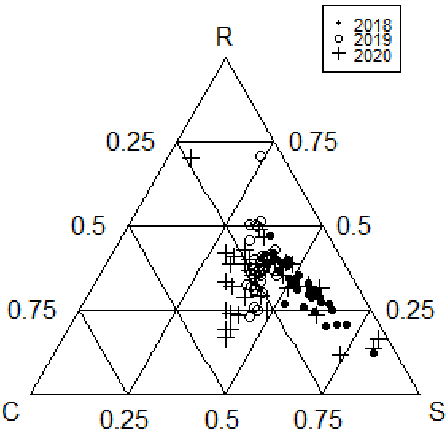


Figure 6: Position of the quadrats of the extensive green plots of the TERRA building in a C-S-R diagram, according to the community percentage of investment in each strategy for the year 2020.

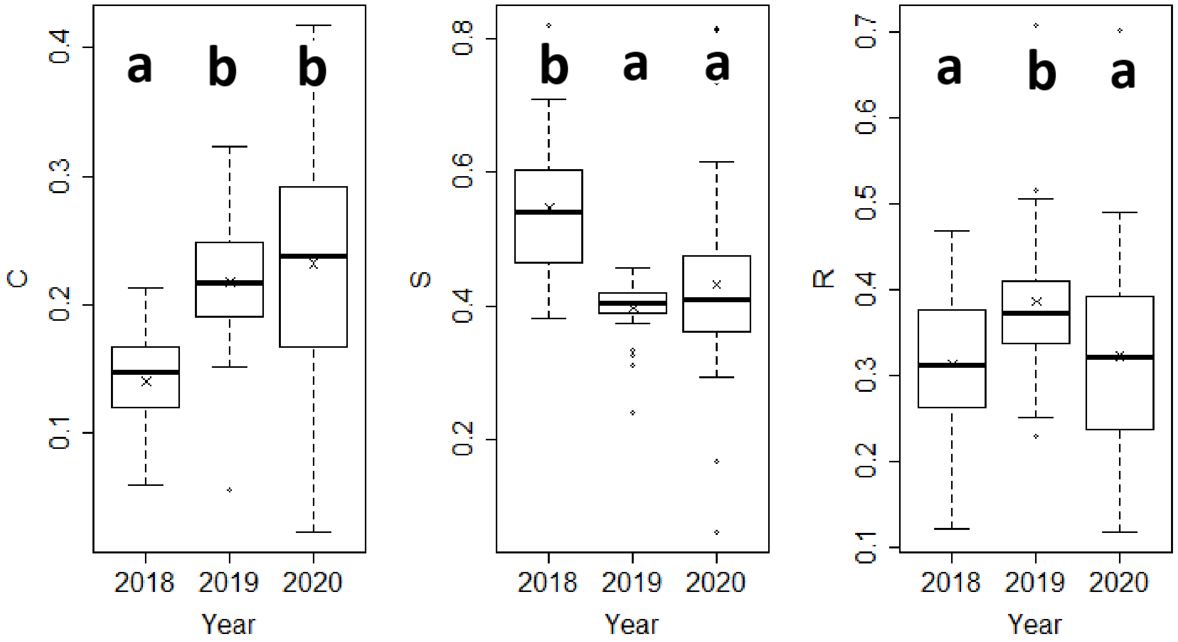


Figure 7: Boxplot of %C, %S and %R investment of plant communities from the extensive green roof plots (n= 36) of the TERRA building, from 2018 to 2019. Black crosses represent mean variables.

4.3) LHS assessment in relation to environmental factors

The interaction of substrate depth and sun exposure affected mean SLA (*p* < 0,01). In 11 cm deep quadrats, mean SLA differed significantly (*p* < 0,01) between low (2273,3 mm^2/mg ± 789,8 mm^2/mg) and high (1564 mm^2/mg ± 837,2 mm^2/mg) or medium exposure (1695,8 mm^2/mg ± 485,0 mm^2/mg). Exposure was not a significant factor in 6 cm deep quadrats (1614,5 mm^2/mg ± 915,3 mm^2/mg, *p* > 0,05). The effect of the year was highly significant (*p* < 0,001), with a decrease in 2020 (fig.8). Each modality follows a similar evolution over time except for the combination of a thick substrate and low exposure, in which two quadrats completely differ from the general trend (fig.8).

Mean canopy height was significantly different (*p* < 0,001) between 6 cm deep (17,0 cm ± 10,3 cm) and 11 cm deep (20,1 cm ± 8,8 cm) quadrats. It was not affected by sun exposure (*p* > 0,05). Mean canopy height was affected by the year (*p* < 0,001). There was an increase in 2019, followed by a decrease in 2020. Seed mass was not affected by any factor and had a high variability (158, 39 mg ± 350,25 mg, fig.9). One quadrat showed an extreme value (3678 mg). This quadrat had a 97% of *V. Sativa,* whose seed mass is 49 mg.

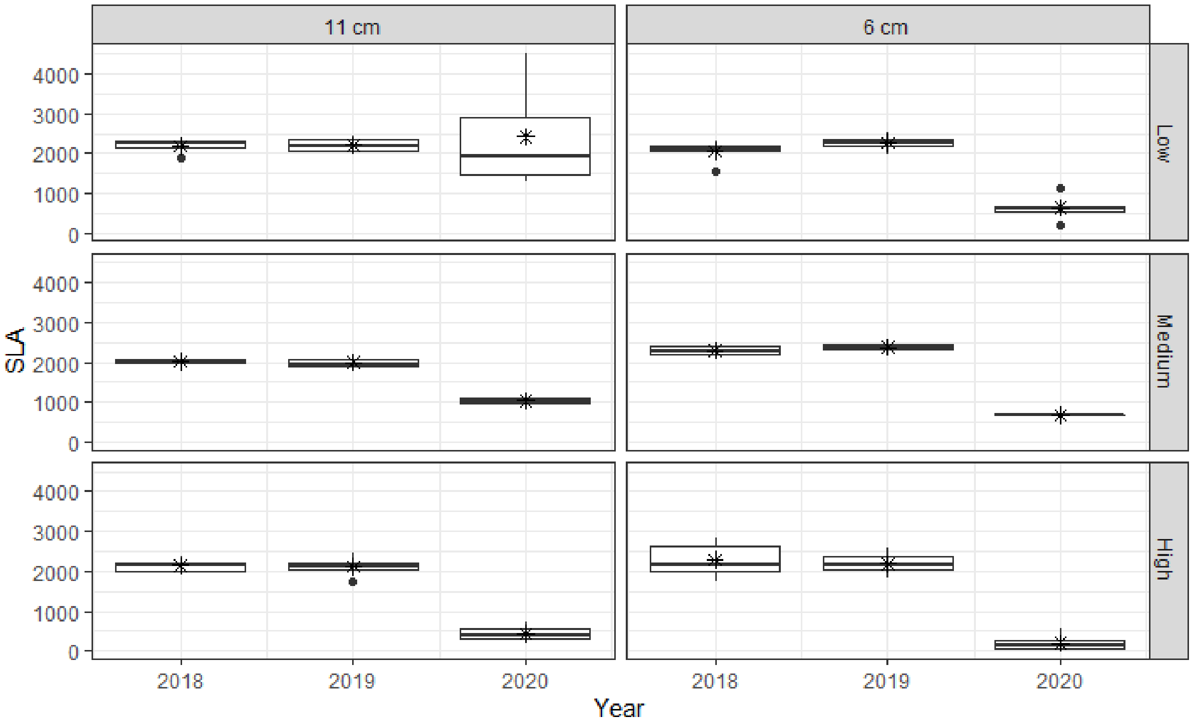


Figure 8: Boxplots of weighted community SLA of the extensive roof plots (n=36) of the TERRA Building (Gembloux), from 2018 to 2020. Black stars represent the observed mean SLA of each combination of substrate depth and class of sun exposure.

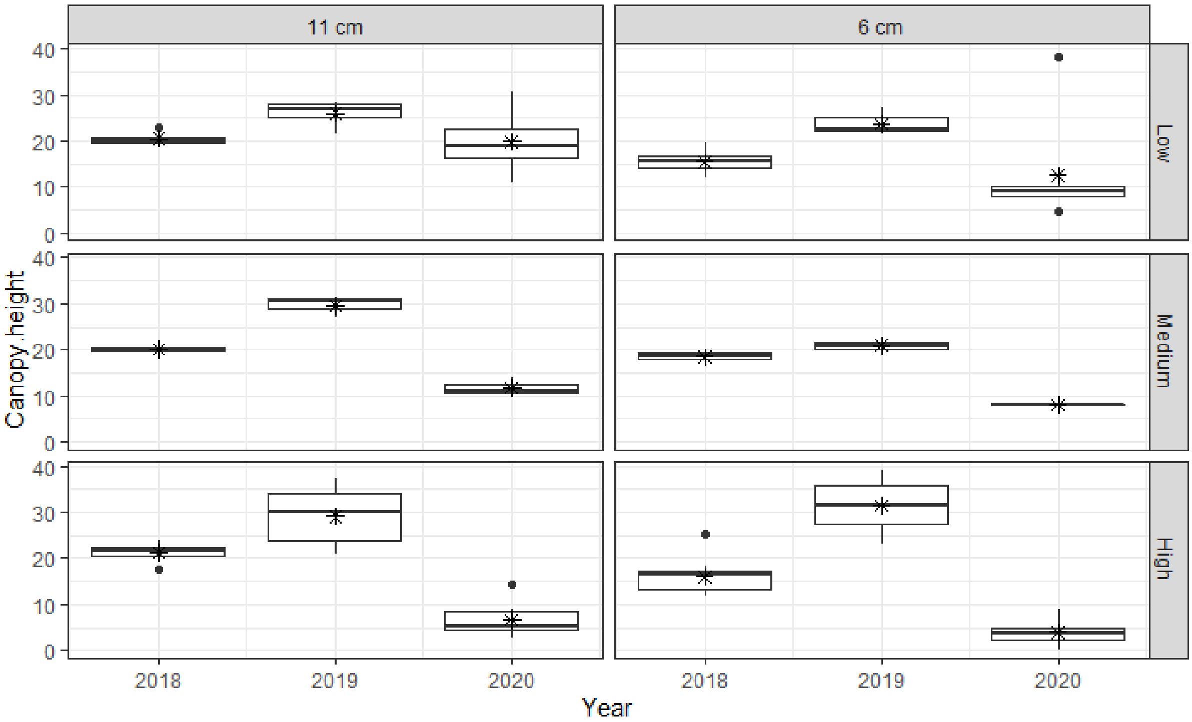


Figure 9: Boxplots of weighted community canopy height of the extensive roof plots (n=36) of the TERRA Building (Gembloux), from 2018 to 2020. Black stars represent the observed mean SLA of each combination of substrate depth and class of sun exposure.

4.4) Moss cover

Mean moss cover was affected by sun exposure (*p* < 0,001) and substrate depth (*p* < 0,01). Mean moss cover was significantly different between low exposure (17,5% ± 7,5%) and both medium (84,5% ± 13,4%) and high exposure (84 % ± 20,4%). Moss cover in thin substrate (54,2 ± 35,6%) was significantly higher than in thick substrates, which (39% ± 36,0%).

4.5) Soil structure and composition

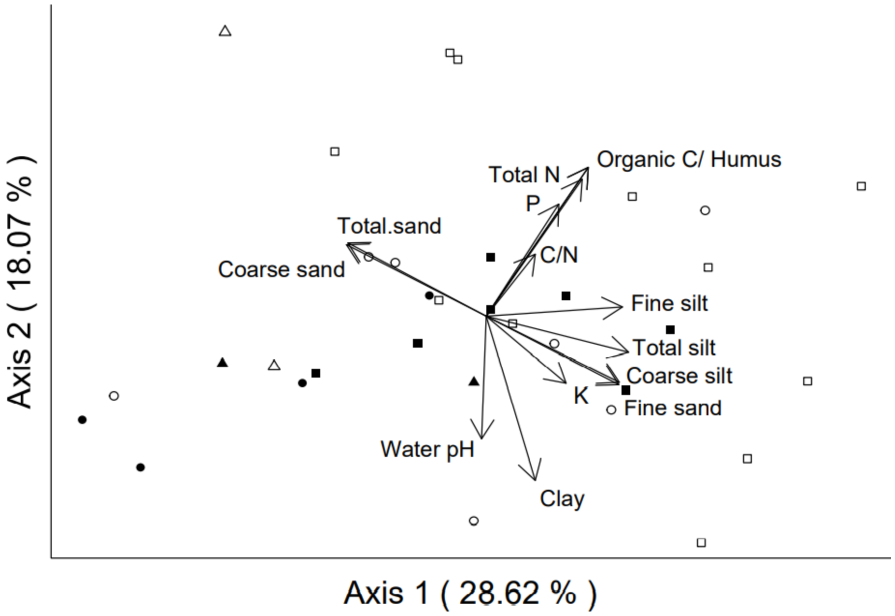


Figure 10: Principal component analysis of extensive green roof substrate of the TERRA Building (Gembloux, n=36), three years after settlement (2020). Symbols represent samples from different exposures (circle= low, triangle= medium, square=high) and depths (white symbol= 6 cm, plain symbol= 11 cm)

The PCA (Axis 1= 28,62%; Axis 2= 18,07%, fig.10) suggested a relationship between fine (% fine silt), coarse (% coarse silt) and total silt percentage (%silt) as well as with fine sand percentage (% fine sand). These variables are positively correlated with the first axis but are negatively correlated with coarse sand (% coarse sand) and total sand (% sand). The PCA also shows a strong correlation between organic carbon/humus (C), total nitrogen (% N), phosphorus (P) and C/N ratio, which all are positively related to the second axis. This axis is also negatively related to water pH and clay percentage ($\%clay$). Potassium (K) has an intermediate position that is linked to positive coordinates on the first axis and negative coordinates on the second.

A significant difference was observed between mean %silt (*p* < 0,001) in high (17,8% ± 3,3 %) and low exposure quadrats (14,9% ± 2,8 %, table 1). Mean C was also higher (*p* < 0,05) in highly exposed quadrats (20,9 g/kg ± 2,0 %) than in low exposure quadrats (18,1 % ± 2,0 %).

Mean water pH (7,9 ± 0,05) was influenced by substrate depth (*p* < 0,001). However, the difference between the two modalities was only of 0,1 pH unit, which is too small to generate differences in ecological responses of the communities. Mean %sand and %clay were not significantly influenced by any of the two factors (p-values > 0,05; %sand = 77,6 ± 3,4; %clay = 5,9 ± 0,9). Mean K content (84,8 mg/ 100g ± 18,0 cm) exhibited an erratic pattern. None of the quadrats contained any CaCo3.

Table 1: Mean values and standard deviation of soil parameters of the substrate of the extensive roof of the TERRA building (Belgium), according to substrate depth and exposure modalities. Values that are in bold represent tests for which p < 0,05. Different letters indicate significant differences.

	Depth		*Exposure*			
	6 cm	*11 cm*	*Low*	*Medium*	*High*	*Interaction*
	Mean	*Mean*	*Mean*	*Mean*	*Mean*	*p-value*
	sd	*sd*	*sd*	*sd*	*sd*	
Water pH	**7,8 (a)**	**7,9 (b)**	7,9	7,9	7,9	0,116
	0,1	**0,1**	0,1	0,2	0,1	
C (g/kg)	20,3	19,1	**18,1 (a)**	**18,5 (ab)**	**20,9 (b)**	0,421
	3,1	2,8	**3,9**	**2,3**	**2,0**	
%N	0,1	0,1	0,1	0,1	0,1	-
	0,0	0,0	0,0	0,0	0,0	
P (mg/100g)	15,2	14,7	14,3	14,4	15,5	-
	1,2	1,1	1,1	1,2	1,0	
K (mg/100g)	84,8	84,8	82,0	60,7	92,4	**0,022**
	22,0	12,1	10,0	34,8	8,4	
C/N	19,9	18,6	19,4	19,0	19,3	-
	0,5	0,5	0,8	0,6	0,9	
Clay (%)	5,8	6,1	6,2	5,9	5,8	0,111
	1,1	0,4	0,7	0,7	1,0	
Total silt (%)	17,1	15,7	**14,8 (a)**	**14,9 (ab)**	**17,8 (b)**	0,287
	3,3	2,4	**2,7**	**2,0**	**2,8**	
Fine silt (%)	10,0	9,3	8,7	9,1	10,4	-
	1,5	1,2	1,4	0,8	1,1	
Coarse silt (%)	7,1	6,5	6,2	5,7	7,4	-
	2,1	1,3	1,4	1,5	1,8	
Total sand (%)	77,1	78,2	79,0	79,3	76,5	0,211
	2,6	3,9	3,3	2,6	3,3	
Fine sand (%)	13,7	14,1	12,4	11,4	15,3	-
	4,8	3,8	3,6	5,6	3,9	
Coarse sand (%)	63,5	64,1	66,6	67,9	61,1	-
	8,4	6,3	8,4	8,1	61,1	-

The constrained analysis of principal coordinates (CAP, appendix 5) showed no relationship between soil variation and plant composition variation among quadrats. The permutation tests for the significance of the constrains showed no significance for the model, the axes and the soil parameters (*p*>0,05).

5) Discussion

In this study, we showed that the interannual variation of plant communities was greater than the effect of substrate depth and sun exposure on this extensive green roof, over the first three years after settlement.

In line with previous studies, the taxonomic approach displayed distinct annual plant compositions (Brown and Lundholm, 2015; Rowe, Getter and Durhman, 2012). Total plant cover was higher in 2019 than in 2018 and 2020, suggesting an influence of precipitation deficits (IRM, 2020b) on canopy density, already observed previously (Brown and Lundholm, 2015). Dominant species in 2018 differed from those of 2019 and 2020, which is consistent with other studies showing either an evolutive shift (Brown and Lundholm, 2015) or an interannual variation of dominant species (Rowe, Getter and Durhman, 2012). The same species dominated plant composition in 2019 and 2020 but their cover dropped in 2020. As opposed to previous studies (Brown and Lundholm, 2015; Rowe, Getter and

Durhman, 2012), the species richness did not drop over the time of the study but varied annually. A decrease in the cover of seeded species was observed, in parallel with an increase in the cover of unseeded colonizing species. Colonization of the roof occurred at a lower speed than previous studies (Aloisio *et al.*, 2019; Brown and Lundholm, 2015; Dunnett, Nagase and Hallam, 2008) and mainly concerned ruderal to generalist species. However, *V. sativa* became dominant over one quadrat in 2020, occupying 97% of its surface. This might be a concern for the coming years, as the dominance of colonizing species can either result in a decrease (Brown and Lundholm, 2015; Dunnett, Nagase and Hallam, 2008) or in an increase (Thuring and Dunnett, 2019) of species diversity on green roofs.

In accordance with previous studies (Brown and Lundholm, 2015; Dunnett, Nagase and Hallam, 2008; Thuring, Berghage and Beattie, 2010), we also showed an effect of micro-environmental factors on plant composition. This effect was discernible for both exposure and substrate depth in 2018 but only for sun exposure in 2020. The explanatory power of the axes of the PCoA decreased over time, indicating a temporal decline in the distinction between the different modalities. This implies that heterogeneity among plant communities of different modalities decreased over the course of our study. This result differs from a longer-term study (Brown and Lundholm, 2015), where the distinction among micro-scale factors increased with time.

The functional approach also revealed significant interannual variation. The C-S-R model indicated an evolution from the stress-tolerant species sown in 2017 towards a more competitive plant composition over time. This follows the assumption of a shift from stress-tolerant pioneer species to more competitive species during primary succession (Grime, 2001). We did not expect this evolutionary trajectory, as extensive green roofs are assumed to keep the primary stage permanently (Lundholm, 2006) and as the original community did not comprise any competitive species. Our result contrasts with longer-term studies, which indicate a dominance of either generalist or stress-tolerant to ruderal strategies (Catalano *et al.*, 2016; Thuring and Dunnett, 2019) after settlement. The short duration of this study does not allow to predict future vegetation as discrepancies were noticed between long-term observations and their chronosequences (Ksiazek-Mikenas and Köhler, 2018).

The implementation of the LHS model to extensive green roof monitoring was not found in literature. Our results showed interannual and micro-scale variations. In the deepest quadrats, mean community SLA decreased with high exposure, following the assumption of a link between a low SLA and stress tolerance (Westoby, 1998). SLA dropped in 2020, which might be in response to the severe drought of April and May 2020. Average canopy height was lower in the shallowest substrate. It might be explained by the lower water reserve of thinner substrates (Chenot *et al.*, 2017; Oberndorfer *et al.*, 2007). It increased in 2019 and decreased in 2020, probably in response to the precipitation rates that was high in 2019 and low in 2020 (IRM, 2020b).

LHS is a specific traits model while the CSR model is a weighted traits approach (Grime, 1977; Westoby, 1998; Hodgson *et al.*, 1999). This means that the global strategy of a plant community may not be directly linked to each component of this strategy. The decrease of the SLA in 2020 reveals one adaptation to stress tolerance, even though the weighted strategy of communities showed an opposite trend. The LHS model was useful to reveal some trends that would have been smoothed out by the CSR system.

Data for 2020 included the cover by dead plants, as the drought had led to the death of most of the species by the end of June. Conclusions on taxonomic diversity and community mean strategies for 2020 only reveal the predictive traits of what was able to grow on the roof but not of what was able to survive until June. Quadrats situated in the same parcel were not independent. The composition of these quadrats possibly influenced one another.

The analysis of moss cover showed that their spontaneous colonization was lower in highly exposed quadrats and narrow substrate quadrats, suggesting an influence of the water reserve of the roof on colonization. Only one study on the influence of micro-scale factors on moss colonization on green roofs was found (Studlar and Peck, 2009). It indicated a taxonomic distinction among different slopes. Further research is needed to determine how substrate depth and sun exposure affect moss composition of green roofs.

The influence of micro-environmental parameters and plant communities on substrate properties has been little investigated. In this paper, we show that micro-environmental factors influenced the chemical and structural properties of the substrate. Organic carbon content and silt percentage were lower in the most shaded quadrats. Green roofs have been shown to experience leaching and degradation (Buffam and Mitchell, 2015; De-Ville *et al.*, 2017), leading to an early aging in terms of structure and organic matter content (Bouzouidja *et al.*, 2018). Further investigation is needed to understand the link between low exposure and degradation of soil properties. We hypothesize that a more favorable environment might have led to a higher carbon mineralization by soil micro-organisms.

The differences in soil parameters were marginal from an ecological perspective. This was confirmed by the constrained analysis of principal coordinates, that showed no link between soil parameters and the plant community response. This means that plant communities and soil parameters both were affected by micro-environmental factors but in an uncoupled way. Substrate was much richer than the soil of calcareous dry grasslands. More specifically, P and K contents were respectively fifteen and fifty times higher than in calcareous grasslands (Piqueray *et al.*, 2011). Soil richness might explain why the stress tolerance strategy was limited as compared to the expectations of the analogous habitat theory.

The plant-soil interactions of extensive green roofs need further investigation in order to optimize their use in green infrastructures. Investigation should focus on water availability and long-term effects of interannual variations. In this study, plant composition surveys occurred in June, which is not representative of the whole growing season. This means that some species might have grown and produced seeds earlier or later in the season. Thus, assessments should be carried out more than once in the season and tolerance to drought events should be considered throughout several growing seasons.

6) Conclusions and perspectives

Green roofs are complex ecosystem, whose range of biotic and abiotic interactions is not well understood yet. This paper highlights the great interannual variation in plant communities and mean plant community strategies. It also points out the effect of micro-environmental factors on both plant communities and substrate properties.

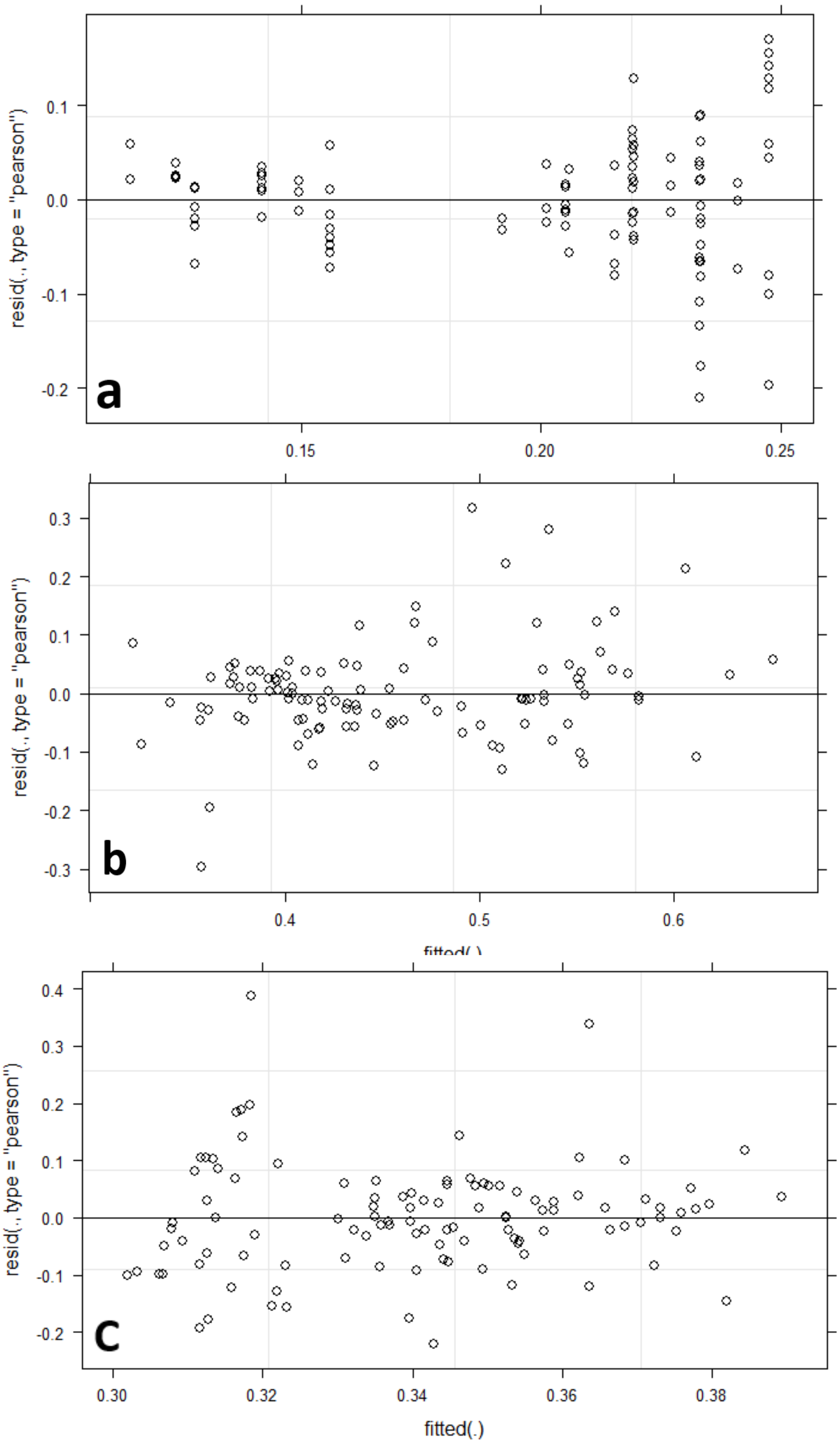
The use of extensive green roofs as habitats of interest in urban environment needs further understanding of the soil-plant complex. The main challenge resides in the creation of plant communities that are capable of withstanding drought events, which are likely to become more frequent with climate change. A better understanding of the effects of drought events on the resilience of green roof plant communities is required.

The selection of species that are known to colonize green roofs in the initial seed mix might be an interesting path to follow, if properly managed. The acceptance of green roofs as dynamic rather than static ecosystem might be the key to a better performance as biodiversity enhancers.

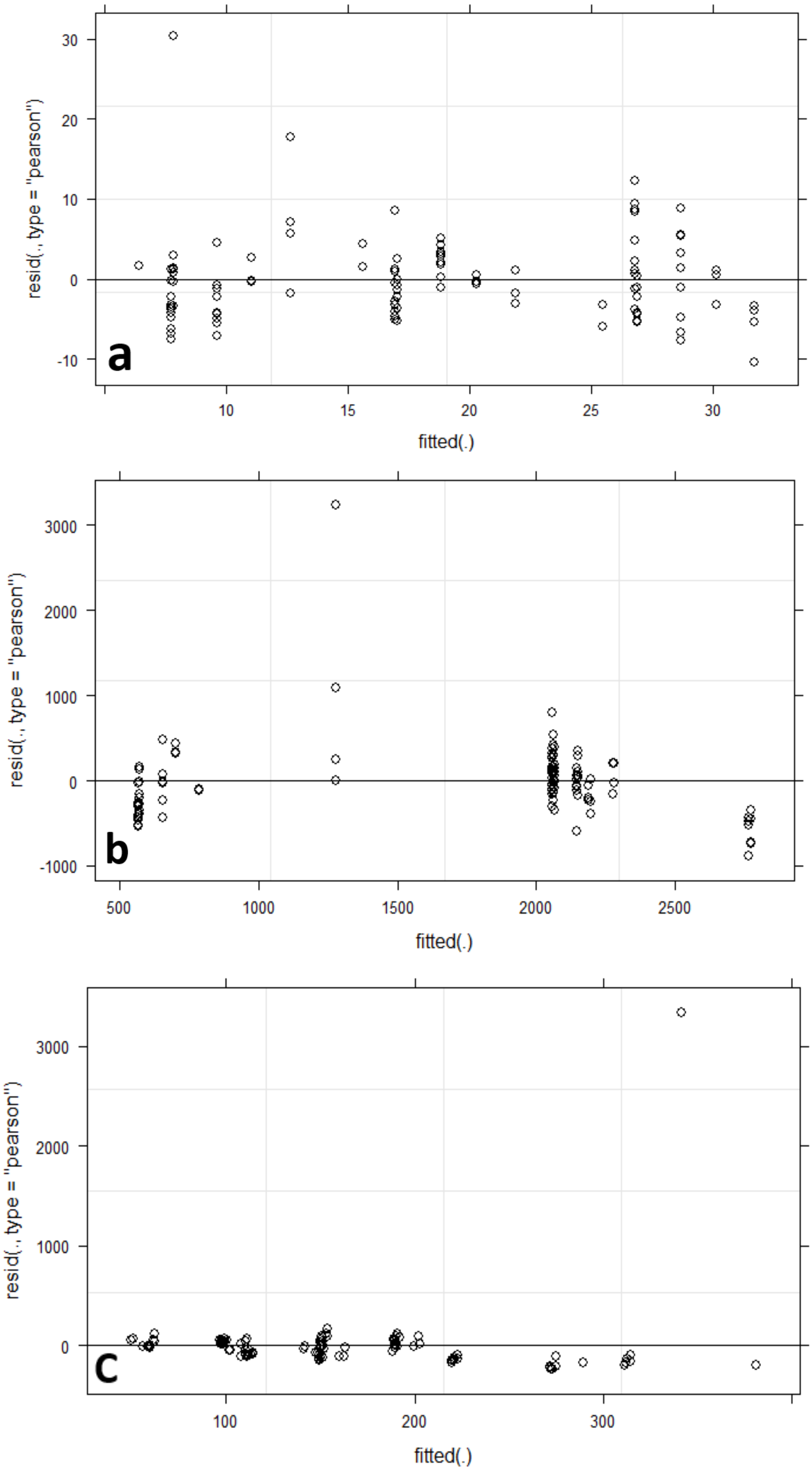
7) Appendices

Appendix 1: Species list and seed density, at the sowing time (2017) of the extensive green roof of the TERRA building (Gembloux).

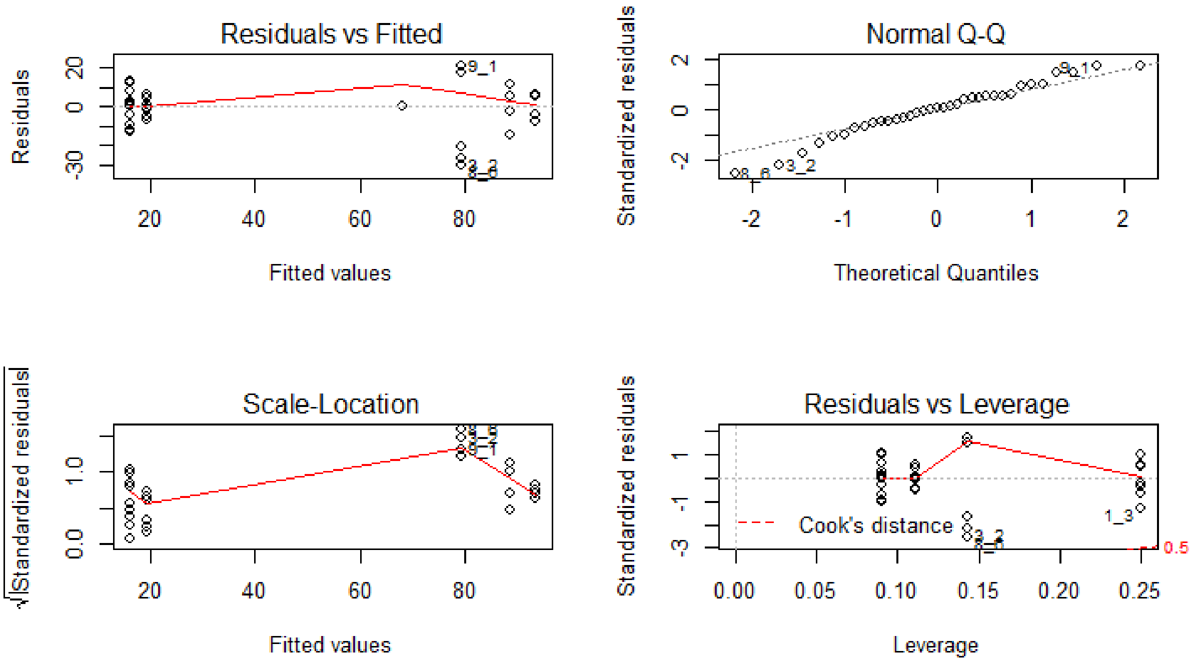
Genus	**Species**	**Density (gr/m²)**
Anthoxanthum	*odoratum*	830
Briza	*media*	830
Poa	*pratensis*	830
Bromus	*erectus*	830
Anthyllis	*vulneraria*	110
Centaurea	*scabiosa*	110
Daucus	*carota*	110
Dianthus	*carthusianorum*	110
Echium	*vulgare*	110
Hieracium	*pilosella*	110
Hypochaeris	*radicata*	110
Koeleria	*macrantha*	110
Leucanthemum	*vulgare*	110
Lotus	*corniculatus*	110
Medicago	*lupulina*	110
Papaver	*argemone*	110
Primula	*veris*	110
Rhinanthus	*minor*	110
Rumex	*acetosella*	110
Sanguisorba	*minor*	110
Scabiosa	*columbaria*	110
Silene	*vulgaris*	110
Thymus	*pulegioides*	110
Tragopogon	*pratensis*	110
Verbascum	*lychnitis*	110
Verbascum	*thapsus*	110
Sedum	*Acre*	110
Sedum	*Album*	110
Sedum	*Rupestre*	110
Total	**26**	**/**



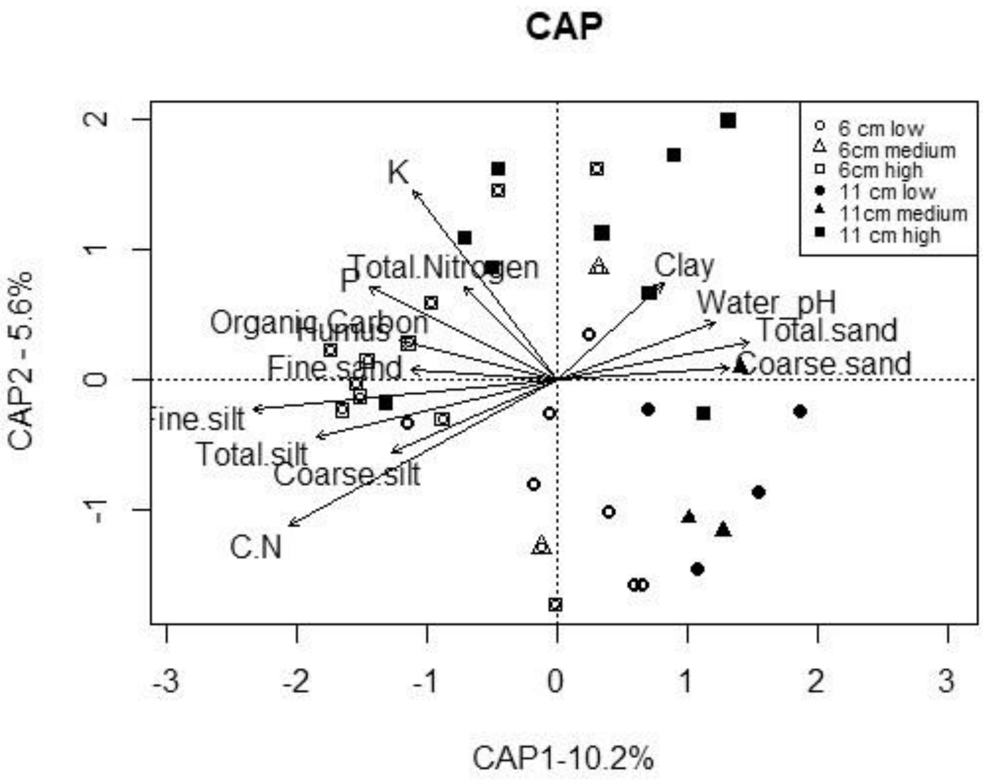
Appendix 2: Fitted residuals of the linear mixed effects models with repeated measures for %C, %S and %R of the vegetal communities (n=36) of the extensive green roof of the TERRA Building (Belgium). a) %C. b) %S c) %R



Appendix 3: Fitted residuals of the linear mixed effects models with repeated measures for the SLA, canopy height and seed mass of the vegetal communities (n=36) of the extensive green roof of the TERRA Building (Belgium). a) SLA. b) Canopy height c) Seed mass.



Appendix 4: Analysis of the residuals of the two-way ANOVA comparing mean moss covers of extensive green roof plots among sun exposure and substrate depth classes (n=36, TERRA building, Gembloux).



Appendix 5: Constrained analysis of principal coordinates of substrate samples (n=36) of extensive green roof plots from different classes of sun exposure and substrate depth (TERRA Building, Gembloux).

Part 2

Foreword: green roofs and plant-pollinators interactions.

1) Introduction

Pollinators play an essential role in ecosystems since the sexual reproduction of most of plant species depends on them (Ollerton, Winfree and Tarrant, 2011). Their economic role is also very important as 35% of the world's plant-based food supply comes from insect pollinated crops (Klein *et al.*, 2007).

In anthropogenic ecosystem, green roofs have been envisioned as a partial solution to halt pollinators decline. They would allow a densification of habitat patches within the urban matrix by providing stepping zones for many taxonomic groups.

However, their success as pollinators enhancers rely on their plant cover as well as on the ability of the targeted groups to access the roof. Local factors influencing green roofs ability to support pollinators include floral resources and visual cues. Some other attractants, such as olfactive cues act on a larger scale. Then, landscape features also play a key role in green roofs performance as a part of green infrastructures.

This combination of factors results in a set of environmental conditions that differs from natural ecosystems. Therefore, plant-pollinators interactions on green roofs need to be evaluated in order to assess their performance and improve their future management.

2) Green roofs as a pollination support

Habitat loss is a key factor in the decline of pollinators, which allows us to envisage the restoration of semi-natural ecosystems or the connectivity between them as a potential solution. Pollinator-supportive restoration must take their feeding distance into consideration as well as their ability to cross inhospitable matrices. It should also consider the ability of plants to settle and form stable communities, that are attractive for pollinators (Menz *et al.*, 2011) .

Low-disturbance management practices and habitat diversity are factors that positively influence some entomological groups in cities (Aguilera *et al.*, 2019; Tommasi *et al.*, 2004; Wastian, Unterweger and Betz, 2016). In this context, extensive green roofs could offer a promising future. Indeed, they generally undergo little disturbance and they allow for the densification of the network of floral offers. They can thus serve as a "stepping zone" in the urbanized matrix (Catalano, Guarino and Brenneisen, 2013).

However, little is currently known about the real benefits of living roofs. A study by Tonieto (Tonietto et al. 2011) indicates a lower rate of visits by bees on green roofs than in parks and urban meadows. Studies comparing the species diversity of roofs with that of the surrounding ground-level environment all indicate equal or higher biodiversity in the latter (Colla, Willis and Packer, 2009; MacIvor and Lundholm, 2011; Tonietto *et al.*, 2011).

Both the position of the roof within the urban matrix and the set of environmental conditions associated to substrate depth and roof exposure can vary greatly. It is therefore important to assess their performance in several contexts regarding their plant composition. To date, plant-pollinators specific interactions have not been studied in real extensive roofing conditions. However, it constitutes a real opportunity to understand the contribution of extensive roofs successful plants to pollinator support.

3) Floral rewards

The sources of nutrients provided by plants to their pollinators are termed floral rewards. Nectar and pollen are considered to be the most important floral rewards (Palmer-Young *et al.*, 2019). Nectar is mainly a source of carbohydrates, while pollen essentially provides amino acids and lipids (Francis *et al.*, 2019).

The three main sugars present in nectar are sucrose, glucose and fructose (Knopper *et al.*, 2016). However, its complete composition, like that of pollen, is more complex. Indeed, these rewards may contain secondary metabolites such as flavonoids, terpenoids, alkaloids and amines, and chlorogenic acids (Palmer-Young *et al.*, 2019).

The complex chemical composition of floral rewards results from a balance between the pollinators attraction and defense against folivores, nectar thieves and pathogenic microorganisms (Dobson and Bergström, 2000; Heil, 2011; McArt *et al.*, 2014). The composition of pollen is also conditioned by its dual role as a gamete and a floral reward. For instance, the presence of alkaloids would reduce pollen predation by bees and increase its probability of fertilization (Muth, Francis and Leonard, 2016).

Each species has a unique chemical profile that may influence its attractiveness and health of different pollinator groups (Palmer-Young *et al.*, 2019). Diversity of floral rewards is therefore of great importance (Potts *et al.*, 2003; Hicks *et al.*, 2016). Indeed, taxonomic groups differ in their requirements for sugar concentrations (Knopper *et al.*, 2016). Pollinators who adopt a licking behavior seem to prefer nectar with sucrose concentration ranging between 50% and 65%. Those who feed by sucking nectar from the nectaries can obtain a fast energy intake with lower concentrations (30% to 40%). Differences in temperature and viscosity also play a role in the preferences of some groups (Knopper *et al.*, 2016).

The quality of floral rewards is not the only factor inferring the probability of interaction between a plant and a pollinator. The accessibility of the resource also influences the rate of extraction of this reward. The latter corresponds to the ratio of the resource harvested to the handling time (Klumpers, Stang and Klinkhamer, 2019). Some pollinators therefore avoid flowers whose nectarifer tube length is too different from that of their proboscis, in order to accelerate extraction (Klumpers, Stang and Klinkhamer, 2019).

This handling time is also influenced by the presence of floral guides, i.e. patterns of floral traits that facilitate their reward location. For example, temperature or color patterns can guide pollinators to resources (Harrap *et al.*, 2020).

4) Attractiveness

Besides floral rewards, the frequency of interactions is influenced by many other attractiveness factors. There are two main categories of factors: visual and olfactory cues. Visual cues include flower color and size as well as flower density, height and morphology (Knauer and Schiestl, 2015; Knopper *et al.*, 2016; Vázquez, Chacoff and Cagnolo, 2009).

Olfactory cues differ between species and sometimes even between individuals. Scent profiles can be classified according to the similarity of their volatile compounds (Burkle and Runyon, 2019). In contrast to visual cues, scent profile acts at long distances (Raguso, 2008a; Junker, 2016). Attractive odors can originate from intra- or extra-floral nectaries (Nicolson, Nepi and Pacini, 2007) or from other floral parts such as petals, pistils, filaments or anthers.

Visual and olfactory clues are sometimes referred to as "honest signals" because they are considered as indicators of floral rewards. For example, the concentration of phenylacetaldehyde, one of the main volatile organic compounds in *Brassica rapa*, is directly correlated to the sugar level in its nectar. This compound is therefore an indirect indicator of the reward level of an individual (Knauer and Schiestl, 2015). “Honest signals" are related to the associative learning ability of certain taxonomic groups, that can memorize the odors associated with the best floral rewards (Mas *et al.*, 2020; Menzel, 1993; Menzel and Greggers, 2013; Raguso, 2008b; Reinhard, 2004).

5) Urban environments and landscape features

The role of urbanization in the largely admitted pollinator decline remains controversial. Wenzel's meta-analysis (Wenzel *et al.*, 2020) shows that their sensitivity to chemical pollution is higher in intensive agricultural environments than in urban areas. Moreover, urban environments are rich in nesting cavities, dry and warm places and food resources. Some species that specialize in cavity nesting therefore increase in fragmented urban environments compared to intact shrublands (Wenzel *et al.*, 2020).

In contrast, other studies indicate low species diversity and declining abundance of some taxonomic groups in urban areas (Bates *et al.*, 2011, 2014; Desaegher *et al.*, 2017; Eremeeva and Sushchev, 2005; McKinney, 2006). The latter are also characterized by a low proportion of rare pollinators and an abundance of common species (Eremeeva and Sushchev, 2005; Winfree, Bartomeus and Cariveau, 2011).

These contrasting responses are linked to the choice of control environment, the taxonomic group of interest and the type of urban environment concerned. Increases in species richness are often associated with moderate urbanization of rural land, below 50% impermeable surface area, while high levels of densification lead to a decline in pollinators (Wenzel *et al.*, 2020).

The role of habitat loss in pollinator decline is well documented and is mediated by mechanisms of decreasing reproduction and survival rates (Winfree *et al.*, 2009). These include loss of feeding and breeding grounds, population subdivision resulting in greater genetic and demographic stochasticity and disruption of interspecific behavior and interactions (Fischer and Lindenmayer, 2007).

As a response to habitat loss, green roofs seem to have a promising future. However, their performance does not only rely on their plant cover but also on the city's landscape features. The proportion of surrounding green spaces (Hennig and Ghazoul, 2011; Tonietto *et al.*, 2011; Wu, 2019) and their connectivity (Wu, 2019) both influence positively species richness and abundance of green roofs.

An end-of-study work carried out in Belgium, at Gembloux Agro-Bio Tech (Froment, 2017) also underlines the importance of the proportion of green spaces in the assembly of bee communities. It highlights the negative relationship between the sedum surface on the roof and the presence of bees. This work also points out the homogeneous and generalized nature of arthropod communities at the scale of the studied roof network. This result is consistent with the literature, which indicates a lower proportion of specialist species on green roofs than on surrounding green spaces (Baldock, 2020; Hofmann and Renner, 2018).

Despite the generally lower diversity of green roofs, green roofs sometimes host rare species, supporting their potential to support biodiversity (Brenneisen, 2006; Kadas, 2006; MacIvor and Lundholm, 2011; Madre *et al.*, 2013).

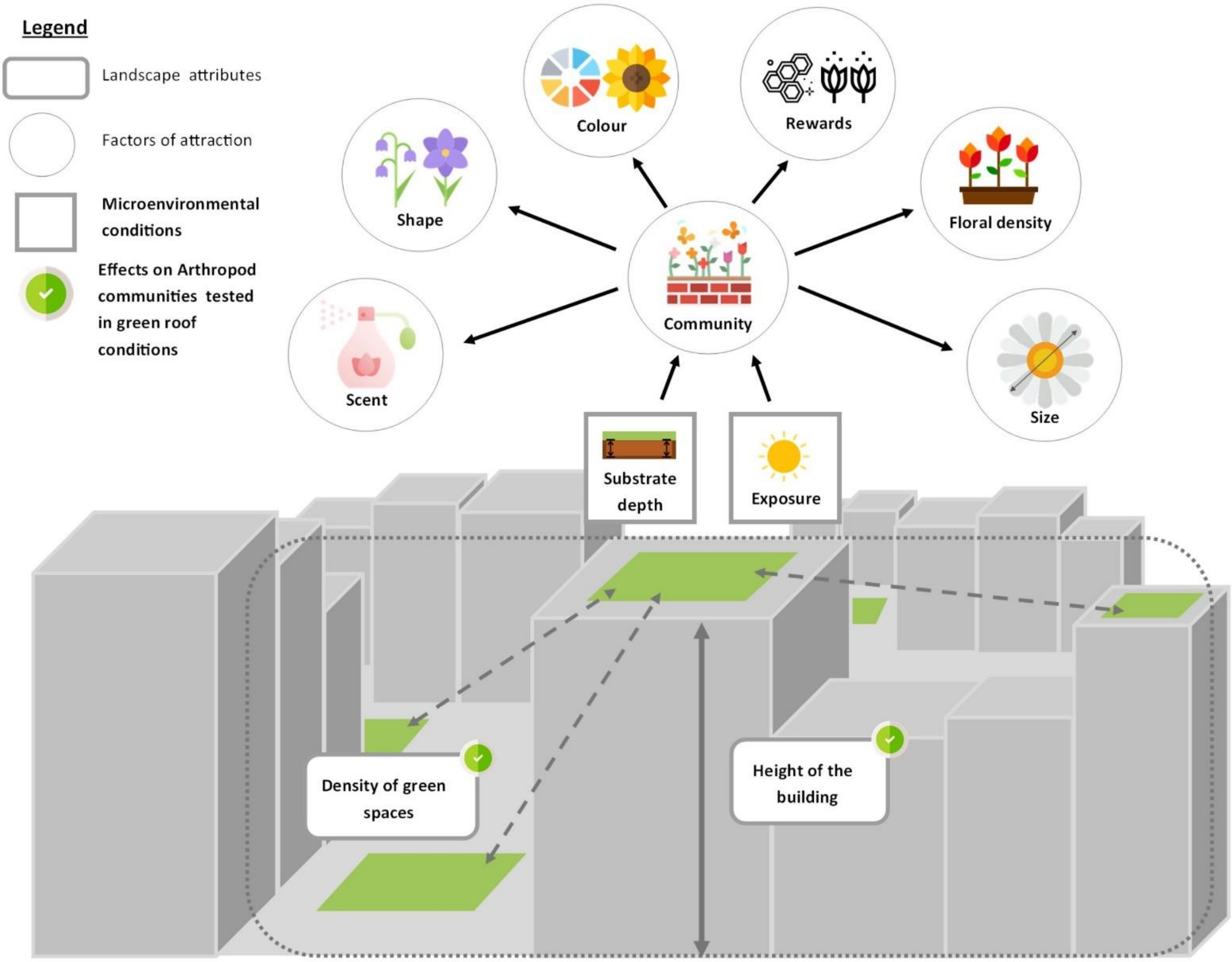


Figure 1: Summary of the factors influencing pollinators attraction and access to green roofs (A. Delruelle, 2020).

6) Pollinator networks

Plant-pollinator networks are called mutualist because of their beneficial interdependence. This means that the maintenance of both insects and plants depends on that of the other. In some cases, it is therefore difficult to determine whether the decline in pollinators is caused by a decrease in the flower supply or whether it is caused by a decrease in the pollination service (Biesmeijer, 2006).

Studying these networks enables the understanding of these interdependent relationships at both plant and animal species level by associating characteristics related to their level of specialization. It also provides information on the stability or structuring elements of the community.

Relationships between pollinators and plants are in most cases asymmetric, with specialized plants generally being visited by generalist pollinators and specialized pollinators generally having generalist host plants (Basilio *et al.*, 2006; Bascompte *et al.*, 2003; Petanidou *et al.*, 2008; Stang, Klinkhamer and van der Meijden, 2007; Vázquez and Simberloff, 2002).

The study of plant-pollinator networks most often consists of collecting the number of interactions between a plant species and an insect. These are observed using sampling units defined by a surface area and a collection time. Since identification in the field is generally impossible for certain taxonomic groups, selective capture is usually carried out.

7) Level of specialization

Several studies indicate that pollinating insects are generally more specialized than pollinated plants (Memmott, 1999; Dupont, Hansen and Olesen, 2003; Menz *et al.*, 2011).

However, it seems that the level of specialization of pollinators has been strongly overestimated. Indeed, most pollination studies are carried out within the same year (Petanidou *et al.*, 2008). A four-year follow-up confirmed the opportunistic nature of plant-pollinator relationships. It challenges the belief that these relationships are both a highly specialized mutualism and a close co-evolution between species. Moreover, the degree of specialization is often biased due to insufficient sampling. Indeed, analyses of the pollen carried by captured specimens highlight floral visits that are not observed in methods consisting of counting interactions over a given period (Bosch *et al.*, 2009).

The level of specialization of a pollinator also depends on how the term is viewed. Firstly, a specialist can be defined as an insect that only visits a limited number of floral species. Secondly, it can be defined as a pollinator with little overlap in resources with other pollinators. Thirdly, it can be viewed as the level of deviation from a generalist network (Dormann, 2011).

Several indices such as connectance, connectivity, modularity or nestedness may give an overview of the level of specialization of the network or in some of its subsets. However, the interpretation of these metrics is difficult and a schematic illustration contains information that may be more likely to be well understood.

Experimental contribution: Plant-pollinator network in real extensive green roof conditions.

1) Abstract

Extensive green roofs are envisioned as a partial solution to halt pollinators decline in urban environments. However, little is known about the interaction between plant and pollinator communities on green roofs. Plant-pollinator interactions have been recorded in twelve transects of an extensive green roof, in Southern Belgium. Transects had an heterogenous setting comprising two depth classes and gradient of sun exposure. Data was collected once a week, from late May to early July 2020, during 7 min transect walks. Captured individuals were identified to the species level, revealing a low species diversity on the roof. An overlap in the feeding niches of the pollinators revealed that all of them were generalist species, at the network level. *Sedum album* and *Echium vulgare* mainly attracted bumblebees at the beginning of the season. *Dianthus carthusianorum* and *Daucus carota* mainly attracted hoverflies at the end of the experiment. A low number of visits by other wild bees has been recorded as compared to bumblebees and hoverflies. A gap in flower resources and in the number of collected visitors was observed in June. Our results suggest that a higher plant diversity is required in order to provide continuous floral resources for to a pollinator community that evolves throughout the season.

2) Introduction

Pollinators play an essential role in ecosystems since the sexual reproduction of most of plant species depends on them (Ollerton, Winfree and Tarrant, 2011). The role of urbanization in their largely admitted decline remains controversial. Urban environments suffer less chemical pollution than agricultural land (Wenzel *et al.*, 2020) and are rich in nesting cavities, feeding resource and dry and warm places. However, they are also characterized by a low species diversity and by the decline of some taxonomic groups (Bates *et al.*, 2011, 2014; Desaegher *et al.*, 2017; Eremeeva and Sushchev, 2005; McKinney, 2006).

Green roofs have been envisioned as a partial solution to halt pollinators decline in urban environments by densifying the urban matrix with habitat patches. To be successful, this strategy must be scaled to the ability of pollinators to cross inhospitable matrices. It should also consider the ability of plants to settle and form stable communities, that are attractive for pollinators and that respect their feeding distances (Menz *et al.*, 2011). It should also provide enough floral rewards to meet the dietary requirements of different taxonomic groups of pollinators (Knopper *et al.*, 2016).

Studies comparing pollinator diversity of green roofs with that of the surrounding ground-level environment all indicate equal or higher biodiversity in the latter (Colla, Willis and Packer, 2009; MacIvor and Lundholm, 2011; Tonietto *et al.*, 2011). However, these studies usually overlook the importance of the plant community composition of the roofs and the commonly used pan traps do not allow to report plant-pollinators interactions.

Extensive green roofs are often covered with exotic species, especially *Sedum* spp. However, S*edum* species based green roofs were demonstrated to have a significantly lower bee diversity than those hosting native forbs communities (Tonietto *et al.*, 2011). Bee communities were also shown to be negatively correlated with the *Sedum* spp. cover of green roofs (Froment, 2017). These results indicate the need for further research to create native plant communities on green roofs that provide effective support for pollinators.

To date, plant-pollinators specific interactions have not been studied in real extensive roofing conditions. However, it constitutes a real opportunity to understand the contribution of extensive roofs to pollinator support.

Studying green roofs performance implies a deep understanding of the factors that influence plant composition and its attractiveness to pollinators. Substrate depth and sun exposure are the most constraining factor for plant development (Brown and Lundholm, 2015). Thus, extensive green roofs success needs to be considered separately from intensive green roofs as they accommodate a lower diversity of plant species (Dunnett, Nagase and Hallam, 2008; Oberndorfer *et al.*, 2007; Rowe, Getter and Durhman, 2012).

Given the diversity of factors involved, detailed plant-pollinator relationships should be examined at the scale of a single roof, taking local context into account.

Studying these relationships allows us to see the contribution of each plant and to adapt the roof's future management. Some plant species might attract a wide diversity of pollinators while some other might host only a few pollinator species. The response of pollinators to the plant community of the roof depends on the level of specialization of both plants and pollinators. Polylectic pollinators are generalist pollen foragers, while monolectic pollinators only rely on one plant species (Rasmussen, Engel and Vereecken, 2020). Pollinating insects tend to be more specialized than plants (Dupont, Hansen and Olesen, 2003; Menz *et al.*, 2011; Memmott, 1999).

However, it seems that specialization of insects is often overestimated, as a one-year sampling usually leads to an overrated degree of specialization (Petanidou *et al.*, 2008).

The level of specialization of a pollinator depends on how the term is viewed. Firstly, a specialist can be defined as an insect that only visits a limited number of floral species. Secondly, it can be defined as a pollinator with little overlap in resources with other pollinators. Thirdly, it can be viewed as the level of deviation from a generalist network (Dormann, 2011).

In a situation where the objective of an extensive green roofs is to enhance the diversity of pollinators, their level of specialization and their rareness at both local and global scales need to be well defined. The contribution of each plant to the network of interactions needs to be understood and characterized in order to improve the floral composition of extensive green roofs.

This paper aims at providing the pollinator network of a native plant composed extensive roof, with a special focus on Antophila (Hymenoptera (Engel, 2005)) and hoverflies. Our objective is to present the diversity of floral visitors from these taxa as compared to their diversity at the local scale and to offer a perspective regarding realized interactions between plant and pollinating species on green roofs.

3) Materials and methods

3.1) Study site

A green roof made of several extensive plots, located in Gembloux (50°33’48” N 4°41’52” E), sown in October 2017 was studied from late May to late July 2020. This set of plots lies on the roof of the TERRA building, at approximately 5,4 m high and is partly surrounded by experimental fields on its eastern side. Gembloux is situated in southern Belgium and has a temperate oceanic climate (Cfb), according to Köppen climate classification (Belgian Federal Service, s. d.). However, 2020 was characterized by an extremely low precipitation rate throughout the whole season (IRM, 2020b).

3.2) Description of the device

The scheme consists of 13 extensive plots (fig. 1), whose size vary from 12 m² to 75 m². The substrate used is "Zinco Extensive Green Roof Substrate©". The initial depth of the plots was either 14 cm (8 plots) or 8 cm (5 plots). Plots have a substrate depth of either 6 (5 plots) or 11 cm (5 plots) after settling.

The plots are oriented East-West and the roof is surrounded by walls on three of its sides (North, East and South). The skylights installed between certain plots create a gradient of north-south exposure of the roof (Appendix 1).

Two sets of species composed of calcicolous grasslands species were sowed in 2017 on different parts of the roof (Appendix 1, appendix 2, appendix 3). The most abundant species of the roof are *Anthoxanthum odoratum* L. and *Bromus erectus* Huds, which are anemogamous. The most abundant entomogamous species on the roof are respectively *Echium vulgare* L., *Sedum acre* L., *Sedum album* L. *and Sedum rupestre* L. *Dianthus carthusianorum* L., *Anthyllis vulneraria* L., *Daucus carota* L. and *Silene vulgaris* (Moench) Garcke are also hosted by the roof but in lower abundance. *Papaver argemone* L., *Rhinanthus minor* L., *Vicia sativa* L., *Medicago lupulina* L., *Senecio inaequidens* D.C, *Sonchus oleraceus* L. and Geranium pusillum L. are the least abundant species.

3.3) Floral visits

Pollinator data were collected in good weather (min 15°C, low wind and no rain) to increase the likelihood of plant-pollinators interactions (Westphal *et al.*, 2008; Lindström *et al.*, 2016).

Sampling were carried out once a week from the 20th of May to mid-July 2020, accounting for 9 sampling days.

Data collection consisted of transect walks. Transect unit was defined by the smallest plot unit of the roof, i.e. 8,6 X 1,3 m (fig.1). Transect units were spread over the roof, proportionally to each combination of sun exposure and seed mix, representing 35% of their surface. Transects were visited in a random order during 7 min, for each sampling day. Hymenoptera from the Antophila clade and hoverflies were the targeted taxa of this study. Other insects that might contribute to pollination were not included. All visits involving physical interaction between a flower and a targeted insect searching for floral rewards were reported in a plant-pollinator matrix. Thus, effective and non-effective pollinators were included but insects displaying a resting behavior were not. The timing was interrupted during the capture of individuals so as not to miss other potential visitors. In every transect, the list of flowering species was recorded on each sampling day to characterize the switches in floral resources throughout the season

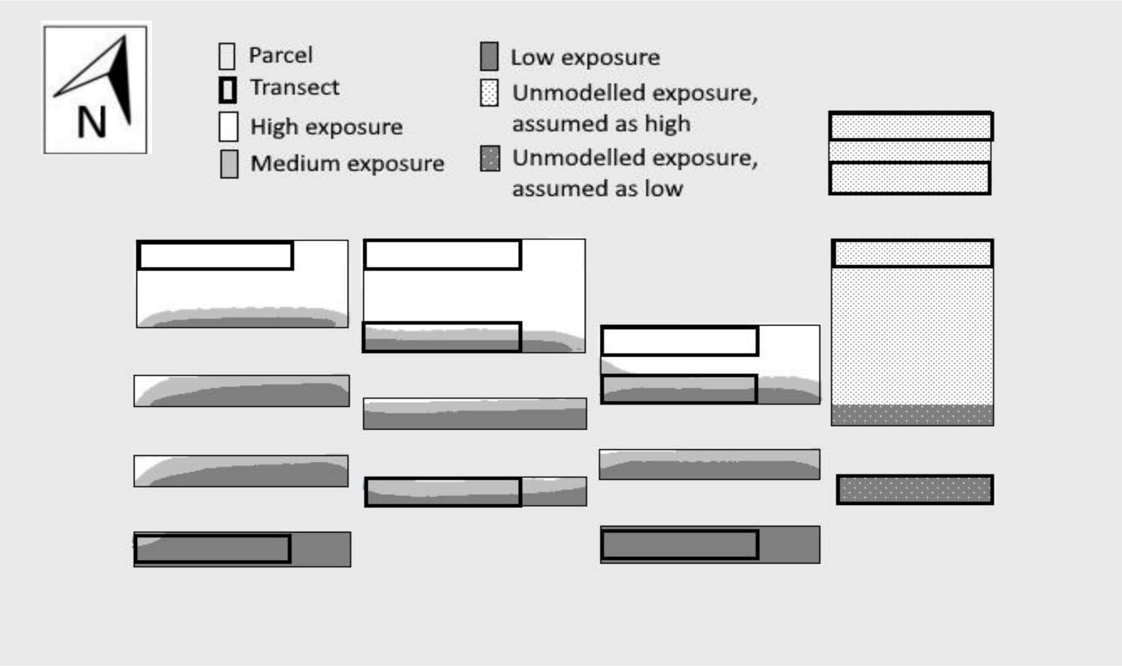


Figure 1: Sun exposure of the roof and sampling transects (TERRA Building, Gembloux).

3.4) Analyses

Description of the network at the roof scale was established, using R 3.6.3 (R Core Team, 2019). The “plotweb” command of “bipartite” package (Dormann, Fruend and Gruber, 2020) offers a metric that represents weighted interactions. The network established in this paper aims to determine how the plant-pollinator interactions on the roof are structured. They are primarily descriptive in nature. Descriptions via connectance or nestedness indices would lack robustness and be difficult to analyze, given the sampling spread over a single season (Petanidou and Ellis, 1993). The network was analyzed visually.

4) Results

A total of 80 individuals were observed on the roof, among which 14 different pollinator species from 5 families (Andrenidae, Apidae, Colletidae, Halictidae, Syrphidae). The most common pollinators found on the roof were *Bombus (Melanobombus) lapidarius* (L., 1758), *Sphaerophoria scripta* (L., 1758), *Bombus terrestris* (L., 1758) *and Bombus (Thoracobombus) pascuorum* (Scopoli, 1793). (fig.3). These species all had interactions with at least three different plant species, with one floral resource outcompeting the others in their number of interactions with the pollinator. *Episyrphus balteatus* (De Geer, 1776) and *Eupeodes corollae* (Fabricius, 1794) had an intermediate abundance on the roof. They had at least three links with floral ressources. *Andrena gravida* (Imhoff, 1832), *Andrena Minutula* (Kirby,1802), *Hylaeus hyalinatus* (Smith, 1842), *Lasioglossum morio* (Fabricius, 1793) and *Sphecodes puncticeps* (Thomson 1870) show a lower total number of interactions and a lower number of links with floral species (fig.2).

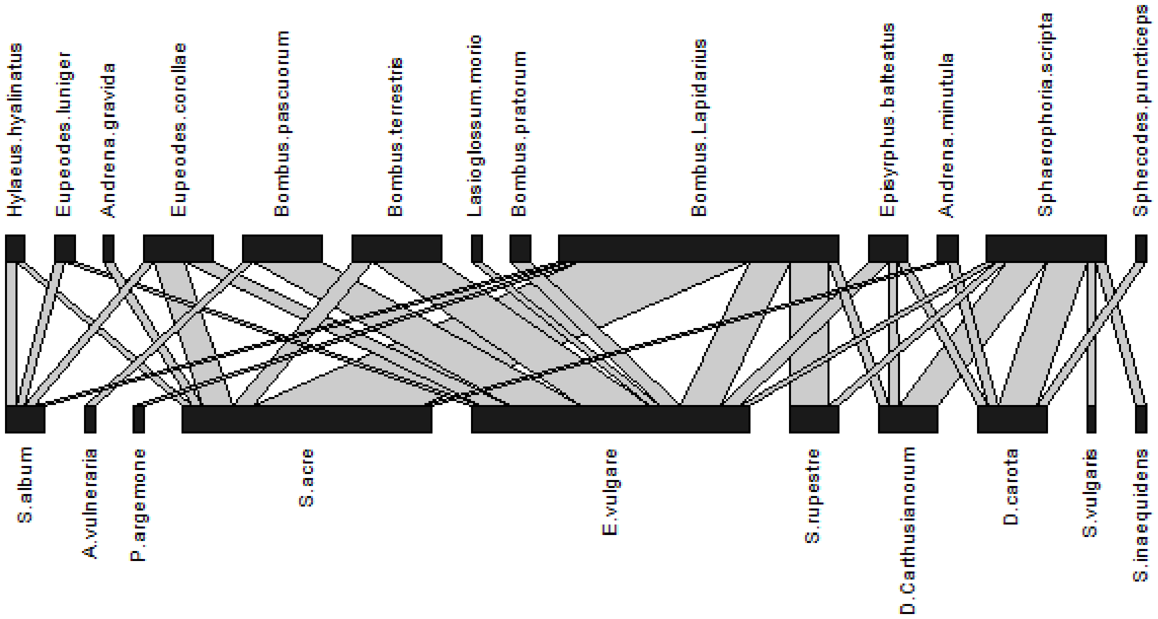


Figure 2: Pollinator network of the extensive green roof of the TERRA building (Gembloux,2020). Upper boxes correspond to pollinators, lower boxes to plant species. The width of black boxes and grey links show the relative importance of the species and of their interactions, respectively.

The main interaction on the roof occurred between *B. lapidarius* and *S. acre*. However, both species shared interactions with several other partners. Interactions on the roof occurred with 10 out of 15 flowering plant species. *E. vulgare* and *S. acre* respectively attracted 9 and 6 different species of pollinators. Apart from being the most attractive species of the roof, they also recorded a higher total number of interactions. *S. album, D. carota* and *D. carthusianorum* all attracted at least 3 different species. *A. vulneraria, P. argemone, S. rupestre, S. vulgaris* and *S. inaequidens* had a low number of total interactions with pollinators and of links with pollinating species (fig.3).

R. minor, M. lupulina, V. sativa and *S. Oleraceus* were present but did not attract any pollinator (table 1). Flowers of these species were observed twice at the most and mostly at a time where the other present species were at peak bloom. The number of transects where they were flowering never exceeded 25 %. The most observed blooming plant throughout the experiment was *E. vulgare*. Its flowering expanded throughout the whole experiment but started dropping in mid-June. The two other most represented plant species were *S. acre* and *S. rupestre.* Both species were in bloom in 50% or more of the transects at the beginning of data collection but also dropped around mid-June. *S. rupestre* and *D. carthusianorum* were in bloom in at least one transect throughout the whole season but in a lesser extent (table 1). *D. Carota* started flowering after mid-June and attracted two species of wild bees and two species of hoverflies (table 1; fig.2).

Table 1: Proportion of transects (n=12) where the presence of a blooming species was recorded in the green roof extensive plots of the TERRA building (Gembloux, 2020).

Date	**S.acre**	**S.rupestre**	**S.album**	**E.vulgare**	**P.argemone**	**D.carthusianorum**	**A.vulneraria**	**S.vulgaris**	**R.minor**	**M.lupulina**	**V.sativa**	**D.carota**	**S. inaequidens**	**S.Oleraceus**
20-05-20	0,50	0,25	0,50	0,67	0,25	0,17		0,17			0,08			
27-05-20	0,50	0,25	0,67	0,58	0,33	0,17	0,17	0,25	0,25	0,08	0,08			
02-06-20	0,50	0,25	0,67	0,42		0,25	0,17							
12-06-20	0,50	0,17	0,42	0,25		0,08	0,08	0,08		0,08				
16-06-20	0,25	0,08	0,33	0,17		0,08								
25-06-20	0,17	0,17	0,08	0,25		0,08	0,08					0,08		
29-06-20	0,08	0,08		0,25		0,17	0,17					0,08		
07-07-20		0,08	0,08	0,25		0,08	0,08	0,08				0,08	0,08	0,08
13-07-20		0,08		0,25		0,17	0,08					0,17	0,08	

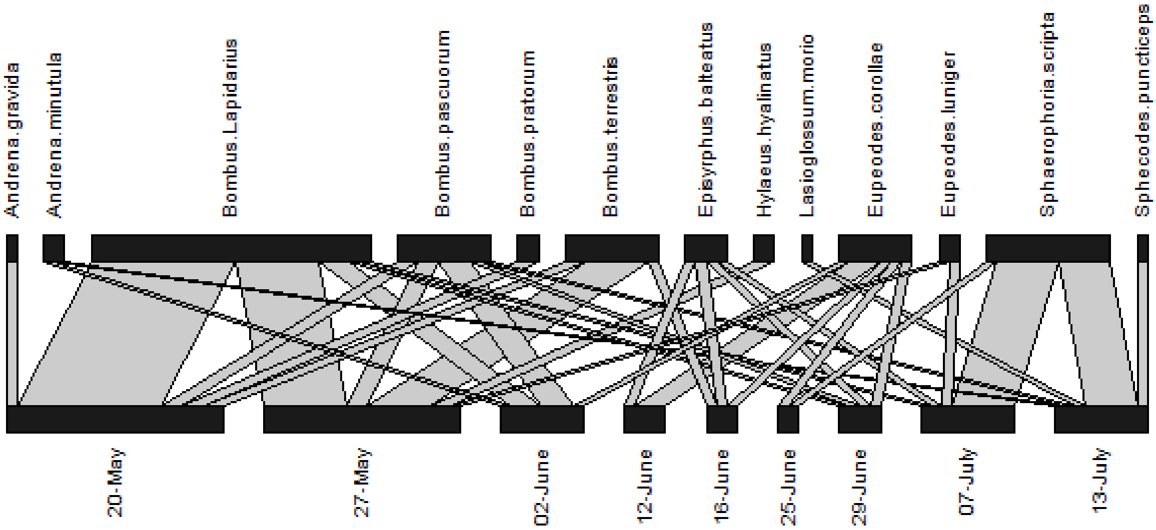


Figure 3: Spreading of pollinators throughout the flowering season on the extensive green roof of the TERRA building (Gembloux, 2020).

Bumblebees were mainly observed on the roof at the beginning of data collection (fig.3). Their presence dropped in mid-June, even though *B. lapidarius* and *B. pascuorum* were still observed in July, in a lesser extent. *B. pratorum* was only observed in May. This was also the case of two wild bees: *H. hyalinatus* and *A. graveda.* Hoverflies were mostly captured on the roof later in the season. *Eupeodes corollae* and *Episyrphus balteatus* reached their peak in June, while Sphaerophoria scripta peaked in early July. No peak was observable for *Eupeodes luniger* (Meigen, 1822). *L. morio* and *S. puncticeps*. were observed once, in early July (fig.3).

5) Discussion

In this assessment of the pollination network of an extensive green roof (TERRA building), only generalist species were collected. Citizen science shows a total of 52 bee species and 46 hoverflies species for the township of Gembloux (*Observations.be*, 2020) against 9 bee species and 4 hoverflies species on the roof. Despite the uncertainty of identification, the bias of detection and the differences in sampling effort and data collection method, we can reasonably assume that the roof's diversity was lower than that of the ground level. Scientific data collected on flower strips with pan traps also show a higher diversity on the ground level, in Gembloux (Amy *et al.*, 2018; Zhou *et al.*, 2016). This is consistent with other studies showing a lower diversity on green roofs than in the surrounding ground-level environment (Colla, Willis and Packer, 2009; MacIvor and Lundholm, 2011; Tonietto *et al.*, 2011).

All the species collected on the roof were found in a least one of the above-mentioned sources about ground level diversity in Gembloux. A decrease was observed in the relative proportion of *E. Balteatus* as compared to *M. corollae* (Hatt *et al.*, 2019; Zhou *et al.*, 2016). However, this change might be observable on the ground level as well and does not lead to the conclusion of a higher attractiveness of the roof for *M. corollae*.

In this study, bee species all were either cavity nesters or ground excavators and all were polylectic (*Atlas Hymenoptera*, no date). Hoverflies species also were generalist species. None of the floral visitors captured on the roof is known to be rare or to be a specialist in terms of dietary requirements, at a global scale (Amy *et al.*, 2018). This is consistent with most of the studies assessing arthropod diversity on green roofs (Baldock, 2020; Froment, 2017; Hofmann and Renner, 2018).

The identity of captured species evolved throughout the season. Bumblebees mainly were captured at the beginning of the experiment and hoverflies mainly were observed at the end of data collection. Local changes in insect communities throughout the season are documented on the ground level as well (Bonnet, 2019; *Observations.be*, 2020). A gap in the number of collected individuals per sampling day was recorder in June, which normally corresponds to the local peak of hoverflies abundance in the season (Zhou *et al.*, 2016; Hatt *et al.*, 2019). This could either be explained by an interannual variation in the season (Williams *et al.*, 2011) related to climatic events or to the observed lack of floral resources on the roof at that time.

The most attractive floral species of the roof were *S. acre* and *E. vulgare*. These species appeared early in the season, providing floral resources for early pollinators, particularly bumblebees. Both species suffered from drought. Their presence started dropping in June, leading to the disappearance of *S. acre*. New cohorts of *E.vulgare* developed later in the season, in low and medium exposure.

From late June to mid-July, only well shaded quadrats still presented flower individuals. Among them, *D. Carota*, followed by *D. carthusianorum* had the highest number of interactions and the highest number of links with pollinator species, especially with hoverflies and wild bees. Since this mid-season period of low floral resources has been reported in similar landscapes (Frankl, Wanning and Braun, 2005), these two species could be of great help in bridging the gap in floral resources at this time.

Plant species appeared to have different roles in the pollinator network. The network was structured by species displaying a high attractiveness, that could be considered as "core species" and by "secondary species" that provided floral resources during blooming gaps. This suggests that a greater plant diversity is likely to better support the pollination network throughout the season. Besides, an increase of plant diversity on green roofs has recently been demonstrated to cause an increase in the diversity of floral visitors (Dusza *et al.*, 2020).

The typology of the whole network showed that the least specialized plant species of the roof attracted the most specialized pollinators. This pattern, known as asymmetric specialization of interaction partners, is well documented in other ecosystems (Bascompte *et al.*, 2003; Stang, Klinkhamer and van der Meijden, 2007; Vázquez and Simberloff, 2002). An overlap of feeding niches was observed on the roof for most of the species and all pollinators had at least to plant species as interaction partners. This means none of the pollinators exclusively depended on one plant species and thus confirms the generalist nature of the pollinator species at the community level (Dormann, 2011).

Some plant species barely interacted with pollinators, probably because of their lower presence in the quadrats at a time where the most attractive species were at peak blooming. However, it is hard to tell if their level of interaction with pollinators on the roof results of a lower attractiveness or of flower development on the roof. A longer-term study would be necessary to determine if these species will have a better development on the roof over time and if it results in a higher attraction of pollinators. It would also allow a better understanding of the pollination success and its influence on green roof plant communities resilience.

Resilience of plant communities to drought and its consequences on the pollination service should be considered over several growing seasons. This was also suggested by another study conducted on the same roof (Degailler, Mahy and Francis, 2020), in spring 2020 showed that *E.vulgare* individuals had encountered pollination success. However, it showed that pollination success had resulted in a lower production of viable seeds in the most exposed parts of the roof, despite the opposite trend of the previous year.

This study is one of the first to link pollinator species of an extensive green roof to its plant community. It gives a first glimpse of the structure of a pollination network, in connection with a plant community developing under real green roof conditions. A longer-term study with a higher sampling effort should be carried out in order to provide an exhaustive list of the potential pollinators of the roof (Petanidou *et al.*, 2008). It also should be noticed that the roof hosted ladybeetles, grasshoppers and thrips. Their assessment was outside the scope of this study, as their contribution to pollination is documented as secondary (Ollerton, Winfree and Tarrant, 2011).

6) Conclusion and perspectives

In this study, the community of pollinators displayed a low diversity and was only composed of generalist pollinators. Despite an insufficient sampling effort, it can reasonably be considered that this green roof failed at enhancing the local pollinator diversity at the township level during the time of the experiment. However, it did provide floral resources to generalist pollinators at least at some points of the season, despite an extreme drought that probably affected natural habitats as well (Phillips *et al.*, 2018). The support of generalist pollinators might be of greater interest in denser cities as compared to Gembloux, which surrounded by green spaces.

The main challenge in the use of extensive roofs in pollinator enhancement remains the creation of stable plant communities, that withstand extreme climatic events and provide continuous floral resources throughout the season. This could be achieved by a greater diversity of plant species, with differentiated phenologies, as suggested in a recent study (Dusza *et al.*, 2020). *S. acre* and *E. vulgare*, *D. carota* and *D. carthusianorum* showed a great potential for pollinator support at different time in the season. However, this list should be completed by other species in order to increase the floral density and to maintain enough floral resources throughout the whole season. Research should include factors that are related to water stress, such as sun exposure, substrate depth or water retention by the substrate, in order to optimize the impact of extensive roofs on pollination support.

7) Appendices

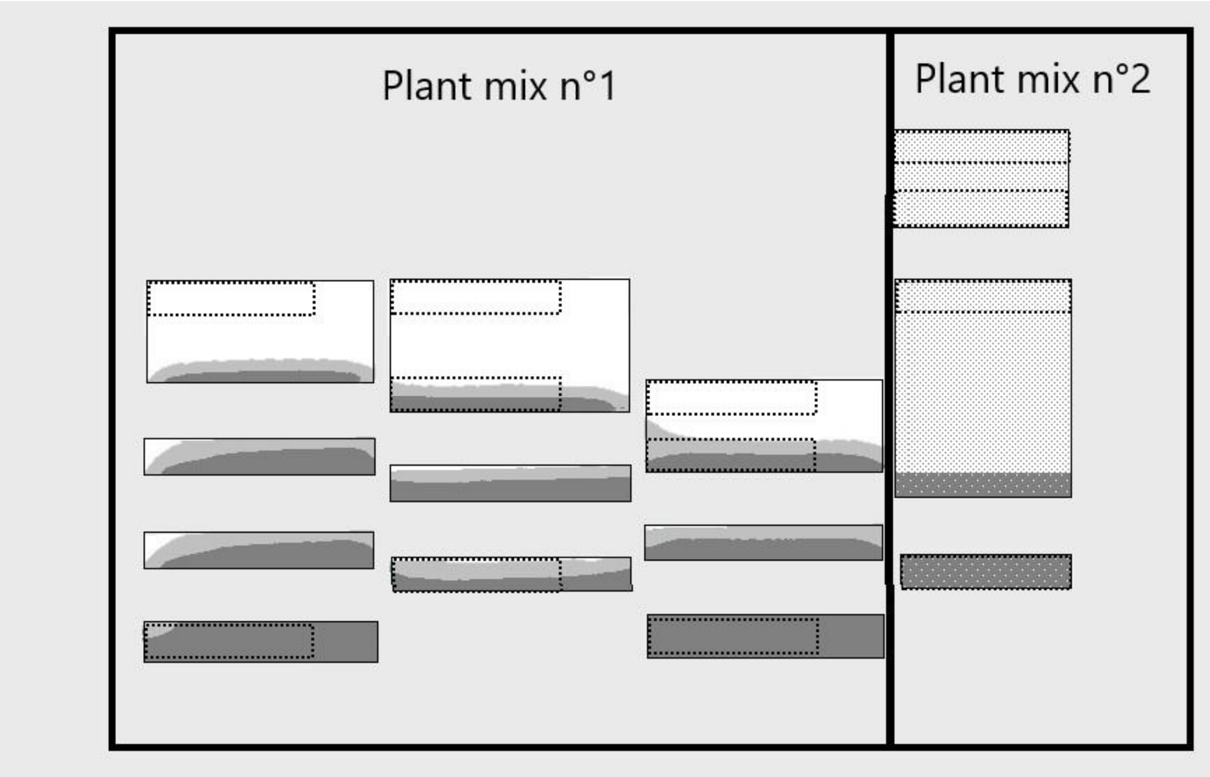
Appendix 1: Species list and seed density, at the sowing time (2017) of the extensive green roof of the TERRA building (Gembloux). Plant mix n°2.

Genus	**Species**	**Density (gr/m²)**
Allium	*schoenoprasum*	10,2
Anthyllis	*vulneraria*	42
Bromus	*erectus*	423
Daucus	*carota*	40,8
Dianthus	*carthusianorum*	31,5
Echium	*vulgare*	108
Medicago	*lupulina*	83,5
Origanum	*vulgare*	5
Papaver	*argemone*	5,5
Poa	*compressa*	40
Rhinantus	*minor*	568
Salvia	*officinalis*	15
Sanguisorba	*minor*	20
Thymus	*pulegioides*	50
Hyssopus	*officinalis*	10
Coriandrum	*sativum*	50
Anethum	*Graveolens*	10
Sedum	*Acre*	110
Sedum	*Album*	110
Sedum	*Rupestre*	110
Total	**17**	**2269,75**

Appendix 2: Species list and seed density, at the sowing time (2017) of the extensive green roof of the TERRA building (Gembloux). Plant mix n°1.

Genus	**Species**	**Density (gr/m²)**
Anthoxanthum	*odoratum*	830
Briza	*media*	830
Poa	*pratensis*	830
Bromus	*erectus*	830
Anthyllis	*vulneraria*	110
Centaurea	*scabiosa*	110
Daucus	*carota*	110
Dianthus	*carthusianorum*	110
Echium	*vulgare*	110
Hieracium	*pilosella*	110
Hypochaeris	*radicata*	110
Koeleria	*macrantha*	110
Leucanthemum	*vulgare*	110
Lotus	*corniculatus*	110
Medicago	*lupulina*	110
Papaver	*argemone*	110
Primula	*veris*	110
Rhinanthus	*minor*	110

Rumex	*acetosella*	110
Sanguisorba	*minor*	110
Scabiosa	*columbaria*	110
Silene	*vulgaris*	110
Thymus	*pulegioides*	110
Tragopogon	*pratensis*	110
Verbascum	*lychnitis*	110
Verbascum	*thapsus*	110
Sedum	*Acre*	110
Sedum	*Album*	110
Sedum	*Rupestre*	110
Total	**26**	**/**



Appendix 3: Allocation of sowed plants compositions on the extensive green roof of the TERRA building (Gembloux).

General conclusion

The results of the extensive roof of the TERRA building indicate a need for further research in extensive green ecology. Despite the encouraging results of the first two years in terms of plant coverage and diversity, the year 2020 was marked by an inability of the roof to withstand more extreme environmental conditions.

The plant community of the roof has not reached a stabilization phase yet and is still mainly driven by interannual variation. Effects of micro-scale factors such as substrate depth or sun exposure are significant but to a lesser extent than the interannual variation.

The study of plant traits did not allow to infirm or confirm the hypothesis that extensive green roofs can be considered as analogous habitats. The CSR model seemed to infirm this hypothesis. However, it also appears that this model might hide some traits that are somehow related to drought resistance and competition.

Our study showed that a slight differentiation of some substrate parameters according to micro-environmental parameters occurs over time. The cause of this differentiation should be investigated in order to maintain substrate quality for plant growth.

The contribution of the roof of the TERRA building to pollinator biodiversity enhancement was quite small for the year 2020. We suggest that a higher plant diversity and abundance are necessary for a continuous floral rewards delivery.

The two experimental contributions of this work bridge together and show that the main challenge of the use of extensive green roofs in biodiversity support remains the creation of plant communities that resist to drought events. The small amount and diversity of pollinators observed in this study probably result from the premature death of most of the plants of the roof. Plant cover and diversity change over time and are very likely to cause varied responses from the pollinator community in the coming years.

This work also connects with that of Degailler, Mahy and Francis (2020), conducted on the same roof, at the same period of the year 2020. Their experimental contribution showed that all the individuals of *E. vulgare* had met pollination success leading to fruit production. However, they showed that individuals from the most exposed parts of the roof had produced non-viable seeds. This means that despite a good pollination service, there is a differentiated success of viable seed production according to sun exposure. Both studies indicate that this species had been particularly successful in the most exposed parts of the roof in the previous year.

This confirms that resilience of plant communities to drought and its consequences on the pollination service should be considered over several growing seasons. Research should keep investigating on how long-term plant communities resist to interannual variations and on the factors that are involved in this resistance. Research on how to create shade on green roofs might be interesting in order to improve growing conditions for plant communities.

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