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Coexistence and Succession of Spontaneous and Planted Vegetation on Extensive Mediterranean Green Roofs: Impacts on Soil, Seed Banks, and Mesofauna

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Abstract: Extensive green roofs are well known to improve the urban environment, but in the Mediterranean regions, dry climatic conditions pose the problem of their sustainability when no irrigation is applied. After planting or sowing in 2012, 18 local Mediterranean plant species on different types of exposure and substrate in a non-irrigated extensive green roof in Avignon (South-Eastern France), the physico-chemical characteristics of the soil, winter and spring soil seed banks, soil mesofauna and initially sown, planted, or spontaneous vegetation expressed on the surface were studied from 2013 to 2020. In 2020, significant differences related to the exposure conditions (shade/sun) and, to a lesser extent, to the depth of substrate used (5 cm/5 cm or 10 cm with a water retention layer) were found. The deeper plots in the shade have significantly higher soil fertility, cover, and vegetation height. However, the plots in the sun have higher moss cover, planted or sowed vegetation abundance, and springtail abundance. By 2020, more than half of the initially sown species had disappeared, except for several planted perennials and short-cycle annual species. On the other hand, a significant increase in the species richness of spontaneously established species was measured over time. In the absence of a permanent and transient seed bank for the sowed and spontaneous species, the plant community is then mostly dependent on species flows via the local surrounding seed rain. Planting perennial species (*Sedum* spp., *Iris lutescens*), followed by spontaneous colonization of species present in the vicinity of the roof would then represent a more efficient strategy for the persistence of extensive non-irrigated green roofs in Mediterranean environments than sowing a species-rich local Mediterranean seed mixture dominated by annual species.

Keywords: geophytes; grassland species; insolation; local species; plant cover; plant diversity; seed rain; substrate depth; survival

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1. Introduction

Nowadays, 55% of the world's population lives in urban areas [1], and the United Nations forecasts an increase to 68% by 2050. Urbanisation converts natural areas to urban areas, impacting ecosystems and biodiversity [1–3]. This shift alters vital services such as climate mitigation, nutrient cycles, water runoff, etc. [1,4,5]. Urban ecology's challenge is sustainability [2], achieved through nature-inclusive design and city greening [6–8] even if it could not replace nature [9]. Rooftops, over 30% of city areas, offer opportunities for novel ecosystems, increased biodiversity, and improved ecosystem services [7,10,11].

Green roofs, e.g., roofs covered by a vegetation layer [7], are known not only for their aesthetic value but also for their numerous environmental benefits that can contribute to the sustainability of buildings and urban areas [7,8]. It has been widely demonstrated that green roofs improve air quality by reducing air pollution and ameliorating roof thermal properties, building insulation and cooling. They can increase the life expectancy of roofs by providing a protective layer from UV radiation and extreme temperatures, offer retention of rainfall, detention of runoff [11], mitigate the urban heat island effect [7,8,12], and promote biodiversity, habitat, and related ecosystem services [7,13,14].

Subsequently, an exponential rise in interest in and implementation of green roofs has been observed during the past decades particularly in temperate Europe and North America [15,16].

In the Mediterranean, semi-arid and arid regions, the study and implementation of green roofs is relatively new and less studied than in the previously cited temperate areas. Nonetheless, their potential to provide significant benefits in high-temperature regions is becoming more evident. It was shown that green roof advantages are also pronounced in the Mediterranean climate [17]. As such, research to improve green roof resilience in these regions is highly valuable and needed [17,18]. Indeed, in Mediterranean semi-arid or arid regions, there are challenges in implementing and maintaining sustainable green roofs [19]. Research on the persistence of plant communities in extensive green roofs has shown that water stress, elevated temperatures, solar radiation, wind, and low substrate depth can negatively impact the growth and survival of plants commonly used for green roof purposes [20] under temperate climates, leading to poor green roof performance and, therefore, discouraging both industry and the government to promote this innovative tool [15,21]. To address these challenges, incorporating local or regional plant species that are adapted to dry climates can improve the resilience of the plant community on green roofs [7]. For example, *Sedum* species are frequently used in green roof applications due to their drought tolerance and regenerative capacities [22,23] and have shown a good establishment with some exceptions [24], but their functional diversity is quite poor [25]. In addition, the use of an appropriate substrate depth and sun exposure conditions can also positively affect soil variables, such as soil fertility, leading to improved plant growth and survival [7,25–28]. However, further research is needed to assess the best implementation strategies and materials in harsh environments to ensure the resilience of plant communities on green roofs in these regions. Moreover, there is a lack of multicompartment studies evaluating not only the vegetation but also soil fertility, soil seed banks, and soil fauna, which are fundamental to soil surface vegetation sustainability and ecosystem services provisioning [7,25,29].

Given the challenges posed by regions with dry climates, many green roofs opt for a deep substrate and irrigation approach, referred to as intensive green roofs [30]. While these green roofs feature a deeper soil layer (15–30 cm) and a diverse range of plant species, including shrubs, trees, and perennial herbaceous plants, they also require more maintenance and irrigation, compared to their extensive counterparts. For this reason, our focus is specifically on the implementation and persistence of extensive green roofs in water-scarce Mediterranean environments [8,29]. Extensive green roofs are characterized by their low weight and low maintenance requirements. They are typically composed of a shallow layer of soil, ranging from just a few centimetres to a maximum of 20 centimetres, and are covered with a variety of drought-tolerant vegetation. These roofs are designed to be relatively self-regulating, relying on rainfall and irrigation to provide water, and they require little maintenance beyond occasional weeding or replanting.

In order to find species adapted to the Mediterranean climate that could be permanently implanted on green roofs, Van Mechelen [25,31,32] undertook to study Mediterranean habitats offering similar conditions in order to draw inspiration from their plant composition (bio-inspiration, habitat template approach, [33]). After having selected 18 different species, an arrangement was then set up on the roofs of the University Institute of Technology of Avignon (Southern Mediterranean France) in September 2012 and surveyed until 2020.

In this study, we explored the green roof ecological dynamics and investigated their relevance in addressing the constraints posed by green roofs in harsh environments. To comprehensively understand the key interactions within this novel ecosystem, we employed a multi-compartment approach in order to shed light on the ecological complexities that shape the resilience of green roofs.

The goals of this study were to assess the persistence of extensive non-irrigated green roofs in Mediterranean environments and to test the effects of substrate depth, structure, and sun exposure by studying specifically the (i) physico-chemical characteristics of the soil, (ii) winter and spring soil seed banks, (iii) soil surface vegetation, and (iv) soil mesofauna for the medium term (i.e., 8 years).

This integrated approach holds the potential to offer valuable insights for optimizing green roof design and management strategies, contributing to the promotion of sustainable urban environments.

2. Materials and Methods

2.1. Study Site and Experimental Setup

In September 2012, 18 experimental plots (1.40 m^2), comprising 3 blocks to reflect heterogeneity, were installed on the rooftop of the University Institute of Technology of Avignon (43°54′36″ N, 4°53′19″ E) in a region characterized by a Mediterranean climate [25].

The same substrate was used for all the plots. It was composed of pozzolana, limestone debris, and organic matter (32 g/L) with a pH of 7.6 with the following nutrient concentrations: nitrogen (33 mg/L), phosphorus (180 mg/L), potassium (700 mg/L), and magnesium (120 mg/L). It had a water retention capacity of 42% The retention layer used was 4 cm thick and made of polyurethane with a high pore rate (98%).

The plots which were separated by a 1 m distance, were arranged in two different exposures: in the shade (30%, given by a shading net) or exposed in full sun and three types of substrates according to different depths and structures: (i) 5 cm substrate, (ii) 5 cm substrate and a water retention layer (WR), and (iii) 10 cm substrate and a water retention layer.

The 3 blocks of the experiment were split into two parts (half-blocks) of which one was shaded (9 plots in total). The three soil treatments were applied to all plots within each of the half-blocks (split-plot design) in order to test the combined effects of exposure and substrate type (18 plots in total).

In each plot, a mixture of 18 commercially different species, previously selected after a screening of dry analogous habitat plant communities such as dry grasslands and rocky habitats [25] was sown (see Appendix A, Table A1).

2.2. Soil Analysis

In January 2020, four soil samples of 50 g were taken at a maximum depth of 5 cm from each of the 18 plots at the four cardinal points, on the edge of the vegetation survey area to avoid any interference before the vegetation surveys were carried out (March 2020). The four samples were then pooled into a single sample per plot and an average sample of 100 g was taken. The soil was air-dried (50 °C) and sieved (2 mm) to be further analysed.

Five parameters related to soil granulometry were measured: % clay, fine silt, coarse silt, fine sand, coarse sand, and 11 parameters related to soil chemistry: calcium oxide (CaO, g kg^{-1}), potassium oxide (K_2O, g kg^{-1}), magnesium oxide (MgO, g kg^{-1}), sodium oxide (Na_2O, g kg^{-1}), cation exchange capacity (CEC, mEq 100g^{-1}), available phosphorus (P_2O_5, g kg^{-1} for a dry soil at 105 °C), total nitrogen (N, g kg^{-1}), carbon to nitrogen ratio (C:N, g kg^{-1}), organic carbon (organic C, g kg^{-1}), total organic matter (OM, g kg^{-1}), and pH. Measurement methods followed the standard protocols, which are described in Appendix B.

2.3. Soil Seed Banks

In January and May 2020, four soil samples of 250 mL were taken from each of the 18 plots in their four corners, at the edge of the vegetation survey area in order to, respectively, survey the winter seed bank (which contains the permanent and semi-permanent seed bank, i.e., seeds that can remain viable in the soil for many years and sometimes decades) in January and the spring seed bank (which contains in addition, the transient seed bank, i.e., seeds that persist in the soil for a relatively short period of time, usually less than one year) in May [34].

A total of 72 samples were therefore taken. As it was impossible to insert a core drill, samples were taken from the same area at the same depth (5 cm) and then placed in a beaker graduated to 250 mL to ensure that the same volume of soil was systematically sampled.

Each sample was then sieved between 2 µm and 2 mm under the water column to remove the largest particles such as stones, and at 2 µm to remove the finest particles such as clays according to the standard protocol of Ter Heerdt et al. [35]. In order to considerably reduce the volume of substrate to be spread, the larger seeds were retrieved from the sieve refuse. The samples were then spread in germination seed trays on a sterile gauze over a substrate composed of 1:3 compost-vermiculite mix to accelerate the growth of the seedlings. The seed trays were then placed under optimal conditions in the greenhouse and watered very regularly, until germination. Seedling species were identified using the flora of Mamarot and Rodriguez [36]. A germination seed tray, without soil samples, was also placed to identify potential seed fallout in the greenhouse.

Viable seed density, species richness, and evenness (J') were estimated.

2.4. Vegetation Survey

In the springs of 2013, 2014, 2016, and 2020, plant mean height, total vegetation cover (%), and cover of both the planted succulent species (*Sedum acre* and *Sedum album*) and bryophytes, as well as the species sown in 2012 and those that had colonized spontaneously were measured according to the protocol established by Van Mechelen [25] in 1 m^2 quadrats in the centre of each experimental plot. In addition, the abundance (i.e., number of seedlings) of both the planted and spontaneously colonized species within the plots were determined. In order to analyse seed bank and plant community data, the species richness (S), evenness (J'), and Simpson index (SDI) were calculated using the *vegan* R package. J' was calculated as $H'/\ln(S)$, with H' being the Shannon diversity index [37].

2.5. Collembola and Mite Survey

Mesofauna was collected using two core-samples from the soil surface (0 to 5 cm deep, 5 cm diameter) within each of the 18 plots in March 2020. Collembola and Acari were extracted using the MacFadyen [38] method over a one-week period and stored in 70% ethyl alcohol. They were counted and sorted under a binocular loupe. Collembola taxa were assigned to life-history groups (epedaphic, hemiedaphic, and euedaphic) according to Gisin [39]. Acari were divided into three suborders: Oribatida, Gamasida, and Actinedida.

2.6. Data Analysis

A split-plot ANOVA was performed to analyse sun exposure and substrate type on individual response variables from the soil, seed bank, mesofauna, and vegetation compartments. Exposure (whole-plot factor) was tested against the block × exposure interaction. The substrate (split-plot factor) and the substrate × exposure interaction were tested against the model residuals.

All models complied with the assumptions of linear models (normality and homoscedasticity). A Tukey HSD post hoc test was calculated to analyse differences between factor levels if factor main effects or interactions were significant (*agricolae* and *multcomp* R packages).

A PCA was computed for soil chemistry variables and plant cover and height with *FactoMineR* and *Factoextra* R packages.

Species composition was compared using NMDS (Non-Metric Multidimensional Scaling, metaMDS function, *vegan* R package) based on the similarity index of Bray–Curtis [40] in order to illustrate changes in plant species composition as well as the species most correlated with each treatment. NMDS analyses were run using 40 random starting configurations in 1–10 dimensions. The run with the lowest stress value was finally applied.

Additionally, partial distance-based redundancy analysis (dbRDA) was applied to evaluate the relationship between divergence in plant community and environmental variables cited above (R package *vegan*).

In order to avoid multicollinearity in environmental data, PCA and Pearson correlation tests between variables were performed on each analysed compartment. Each variable with a correlation higher than 0.90 was removed from the analysis.

Partial dbRDA were fitted separately for the Bray–Curtis distance between vegetation relevés using permutation testing [41]. A marginal test was performed using environmental variables as predictors. The significance of the global model and the environmental variables was evaluated using a dbRDA permutation test (9999 permutations).

All data analyses were run in R software (R, v.4.0.2, R Development Core Team (2020) [42]).

3. Results

3.1. Effect of Substrate and Exposure on Soil Parameters

Substrate and exposure affected both soil granulometry and chemistry but to a different extent (Table 1; Figure 1) in 2020.

Table 1. ANOVA F-values, significance levels for effects of substrate and exposure on (a) soil granulometry and (b) chemistry on an extensive Mediterranean green roof in 2020. S × E = substrate × exposure interaction. $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, NS not significant.

(a) Soil granulometry

	df	Clays	Fine silt	Coarse silt	Fine sand	Coarse sand
Substrate	2	1.22 NS	2.78 NS	2.72 NS	7.37 *	4.13 *
Exposure	1	10.56 *	0.01 NS	0.04 NS	0.01 NS	0.01 NS
S × E	2	7.95 *	0.77 NS	1.88 NS	0.89 NS	2.14 NS

(b) Soil chemistry

	df	CEC	pH	P_2O_5	K_2O	MgO	CaO	Na_2O	Total N	Organic C	OM	C:N
Substrate	2	1.89 NS	0.44 NS	1.22 NS	1.16 NS	6.80 *	5.19 *	3.26	2.87 NS	4.12 *	4.02	0.73 NS
Exposure	1	14.73 *	0.64 NS	28.87 **	37.49 **	106.60 ***	42.27 **	180.20 ***	78.74 ***	139.50 ***	139.50 ***	0.01 NS
S × E	2	1.32 NS	0.80 NS	0.82 NS	0.76 NS	0.63 NS	1.92 NS	1.22 NS	0.29 NS	0.45 NS	0.45 NS	0.09 NS

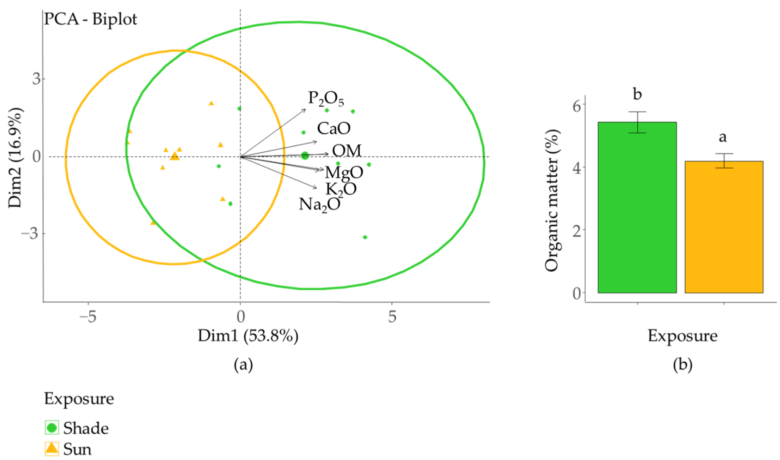

Figure 1. (**a**) Principal component analysis of soil chemistry variables on an extensive Mediterranean green roof in 2020. Ellipses represent a concentration of the score for each vegetation zone with 95% confidence boundaries around group means. (**b**) Effect of exposure on organic matter (mean ± SE). Different lower-case letters indicate significant differences in vegetation zone effect ($p < 0.05$).

Substrate depth affected two granulometry variables, leading to significantly coarser and finer sands in the 5 cm substrate without retention layer.

Exposure and substrate × exposure interactions were significant solely for clay percentage resulting in a higher clay proportion in the 5 cm substrate without retention layer (Table 1a).

Soil fertility expressed by CEC, P_2O_5, K_2O, MgO, CaO, Na_2O, total nitrogen, organic carbon, and total organic matter significantly increased for shade condition and MgO, and CaO and organic carbon showed a differential response to substrate depth as a significantly higher content for these parameters was measured in the 5 cm substrate without retention layer than 5 cm substrate with retention layer (Table 1b).

3.2. Effect of Substrate and Exposure on Seedbanks

A total of 30 species were found in the spring seed bank from which only 6 were planted in 2012. Concerning the winter seed bank, 20 species were observed from which the same 6 species found in the spring seed bank were planted in 2012 (Figure 2, see Appendix A, Table A1).

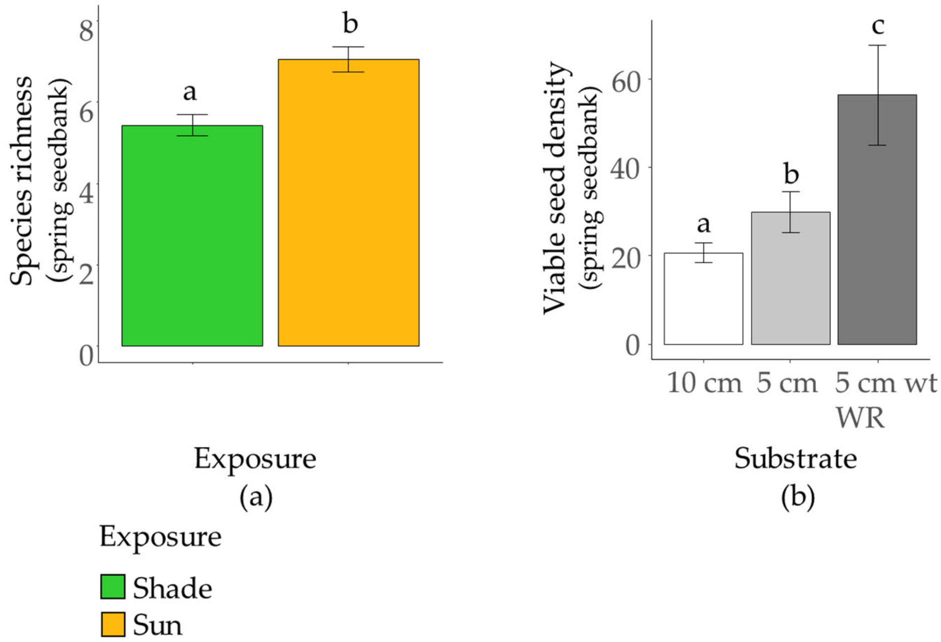

Figure 2. (**a**) Effect of exposure on species richness of the spring seed bank on an extensive Mediterranean green roof in 2020 (mean ± SE). (**b**) Effect of substrate on viable seed density of the spring seed bank (mean ± SE). Different lower-case letters indicate significant differences in vegetation zone effect ($p < 0.05$).

The spring seed bank composition and structure were highly affected by the experiment variables (Table 2; Figure 2). Viable seed density was higher in the 5 cm without retention layer than in the two other substrates. Sun exposure also increased viable seed density. A significant substrate × exposure occurred. In sun exposure, density increased as substrate depth decreased, while in the shade exposure, no difference was found among the substrates. Species richness responded solely to exposure. Richness was found to be higher in the sun exposure. Evenness was affected by substrate and exposure and also by their interaction. Evenness was lower for the 5 cm depth substrate without retention layer. It was also lower for sun exposure. Lastly, the significant interaction is due to a differential response to exposure for the 5 cm depth substrate without retention layer: evenness decreased in the sun exposure.

Table 2. ANOVA F-values, significance levels for effects of substrate and exposure on (a) spring and (b) winter seed banks on an extensive Mediterranean green roof in 2020. S × E = substrate × exposure interaction. $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, NS not significant.

(a) Spring seed bank				
	df	**Viable seed density**	**Species richness**	**Evenness**
Substrate	2	11.33 ***	1.28 NS	11.13 ***
Exposure	1	30.25 **	6.49 *	63.64 **
S × E	2	8.36 ***	0.14 NS	12.13 ***
(b) Winter seed bank				
	df	**Viable seed density**	**Species richness**	**Evenness**
Substrate	2	1.86 NS	2.18 NS	4.41 *
Exposure	1	0.90 NS	0.03 NS	0.02 NS
S × E	2	0.79 NS	2.82	1.17 NS

At the opposite end, the winter seed bank showed a differential response only for the evenness response. Evenness was still significantly lower in the 5 cm depth substrate with retention layer compared to the same depth without retention layer.

3.3. Effect of Substrate and Exposure on Mesological Data, Planted and Spontaneous Plant Community

The total vascular plant cover responded to exposure with a significantly lower cover in the sun condition (Table 3a; Figure 3). The *Sedum album* cover was only marginally affected by substrate and exposure, while the *Sedum acre* cover decreased significantly in the sun and was the highest in the 5 cm depth substrate with retention layer compared to the 10 cm depth substrate. Bryophyte cover was higher in the sun-exposed plots. Neither substrate nor exposure had an effect on mean plant height.

Table 3. ANOVA F-values, significance levels for effects of substrate and exposure on plant community: (**a**) cover and height, (**b**) planted vegetation, (**c**) spontaneous vegetation on an extensive Mediterranean green roof in 2020.

(a) Cover and height						
	df	**Total plant cover**	***S. album* cover**	***S. acre* cover**	**Bryophyte cover**	**Mean plant height**
Substrate	2	0.18 NS	3.80	4.68 *	0.30 NS	2.33 NS
Exposure	1	15.76 *	2.38 NS	20.54 *	20.37 *	4.78 NS
S × E	2	0.16 NS	3.64	0.61 NS	0.98 NS	0.11 NS
(b) Planted vegetation						
	df	**Species richness**	**Simpson index**	**Evenness**	**Abundance**	
Substrate	2	4.73 *	3.22	1.52 NS	11.12 **	
Exposure	1	1.25 NS	6.26	2.15 NS	65.51 **	
S × E	2	1.95 NS	6.51 *	18.70 ***	12.35 **	
(c) Spontaneous vegetation						
	df	**Species richness**	**Simpson index**	**Evenness**	**Abundance**	
Substrate	2	0.43 NS	0.52 NS	0.66 NS	3.29	
Exposure	1	15.00 *	0.42 NS	3.15 NS	87.05 **	
S × E	2	0.95 NS	1.14 NS	0.38 NS	0.92 NS	

S × E = substrate × exposure interaction. $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, NS not significant.

In 2020, only eight species out of the eighteen planted in 2012 were found. We also identified 34 spontaneous species. Planted vegetation was strongly affected by the experimental variables (Table 3b; Figure 3). The substrate had a significant effect on species richness and abundance. The 5 cm substrate depth without retention layer exhibited a lower species richness and abundance than the 10 cm substrate depth with retention layer. Exposure only significantly modified abundance with a higher abundance in the sun. The substrate × exposure interaction was significant for almost all parameters: Simpson index, evenness, and abundance. The Simpson index was higher for the 5 cm substrate depth (with and without WR layer) in the sun than for the 5 cm substrate depth without WR in the shade. Evenness was higher for the 5 cm substrate depth without WR in the sun than for the 5 cm substrate depth without WR in the shade. At least, abundance was higher for the 10 cm substrate depth with WR in the sun than for the others. Spontaneous vegetation (Table 3c; Figure 3) had a mild response to the experiment variables with only a significant effect of exposure on species richness and abundance. These two parameters were higher in the sun.

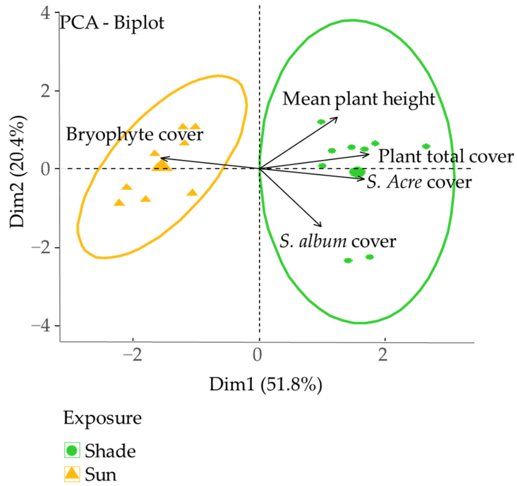

Figure 3. Principal component analysis of plant cover and height on an extensive Mediterranean green roof in 2020. Ellipses represent a concentration of the score for each vegetation zone with 95% confidence boundaries around group means.

In 2020, eight years after the roof installation, NMDS ordination showed a clear separation between the plant community of shade and sun exposure along axis 1 (Figure 4). Axis 2 of the NMDS demonstrated a separation of the plant communities between the three substrates with a stronger effect for sun exposure (Figure 4).

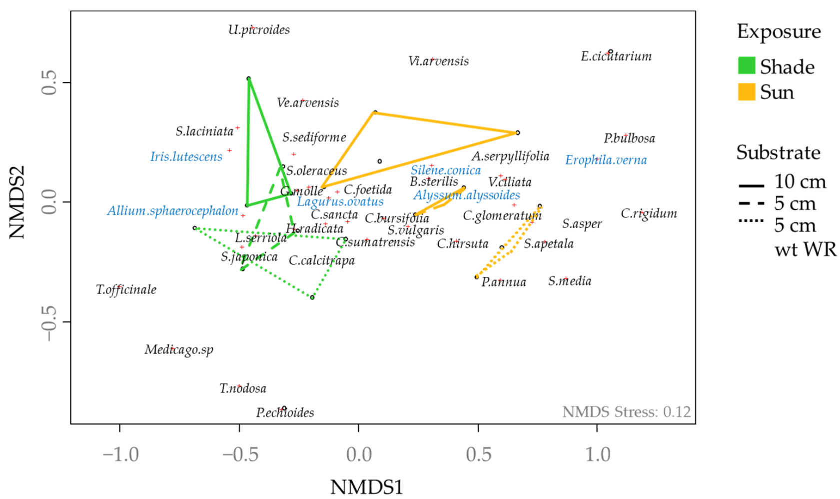

Figure 4. Effect of exposure and substrate on plant species composition from NMDS data on an extensive Mediterranean green roof in May 2020. Polygons indicate the position of the outmost plots in each treatment (two dimensions). Species written in blue correspond to planted species. For species code, see Appendix A, Table A1.

Mean species richness of planted vegetation showed a negative trend while mean spontaneous plant richness showed a sharp increase since 2014 (Figure 5).

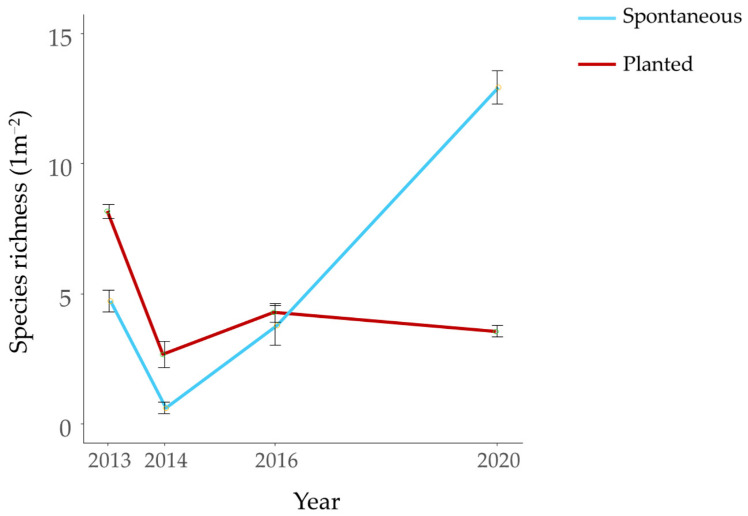

Figure 5. Mean species richness (1 m^2) evolution from 2013 to 2020 for planted and spontaneous vegetation (mean ± SE) on an extensive Mediterranean green roof in 2020.

3.4. Effect of Substrate and Exposure on Collembola and Mite Density

In 2020, total collembola density was influenced by exposure with a higher density in the sun exposure. Total mite density was affected by the interaction substrate × exposure. Density decreased significantly with the decreasing depth of the substrate in the sun exposure while the substrate had no effect in the shade (Table 4, Figure 6).

Table 4. ANOVA F-values, significance levels for effects of substrate and exposure on total collembola and mite density on an extensive Mediterranean green roof in 2020.

	df	Mean Collembola Number	Mean Mite Number
Substrate	2	1.73 NS	2.05 NS
Exposure	1	51.69 *	4.79 NS
S × E	2	0.22 NS	4.90 *

S × E = substrate × exposure interaction. * $p < 0.05$, NS not significant.

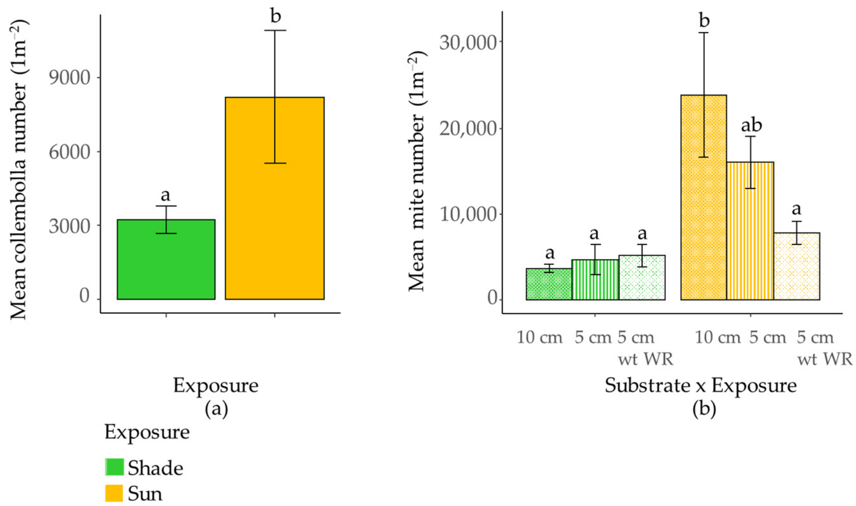

Figure 6. (**a**) Effect of exposure on mean collembola number (mean ± SE). (**b**) Effect of substrate × exposure interaction on mean mite number (mean ± SE) on an extensive Mediterranean green roof in 2020. Different lower-case letters indicate significant differences in vegetation zone effect ($p < 0.05$).

Ecomorphological groups of collembola (epedaphic, hemiedaphic, and euedaphic) were not affected by substrate or exposure as two out of three suborders of mites (Oribatida, and Actinedida). Gamasida and Oribatida (marginally) were the two only groups with a density higher in the deeper substrate (10 cm) (Table 5).

Table 5. ANOVA F-values, significance levels for effects of substrate and exposure on mean collembola and mite number on an extensive Mediterranean green roof in 2020.

(a) Mean Collembola number				
	df	**Epedaphic**	**Hemiedaphic**	**Euedaphic**
Substrate	2	0.07 NS	2.88	0.87 NS
Exposure	1	20.51 NS	23.77 NS	1.42 NS
Substrate × Exposure	2	0.62 NS	0.37 NS	0.85 NS
(b) Mean Mite number				
	df	**Oribatida**	**Actinedida**	**Gamasida**
Substrate	2	2.69	0.67 NS	3.59 *
Exposure	1	1.30 NS	10.20 NS	11.60 NS
Substrate × Exposure	2	1.03 NS	0.83 NS	2.20 NS

S × E = substrate × exposure interaction. $p < 0.1$; * $p < 0.05$, NS not significant.

3.5. Interactions between Studied Compartments in 2020

Concerning planted species, dissimilarity (Jaccard index) between vegetation on the roof and seed bank in 2020 was quite high and showed no change over time from 0.55 to 0.69. The dissimilarity between standing vegetation over the years showed no trend related to time from the roof installation for neither planted nor spontaneous species. This result is the same for winter and spring seedbanks as the same species were found in both.

Spontaneous species showed higher dissimilarity with both seedbanks in 2020 than planted species but also between standing vegetation on the roof (Figure 7). The winter seed bank is more similar than the spring seed bank to standing vegetation.

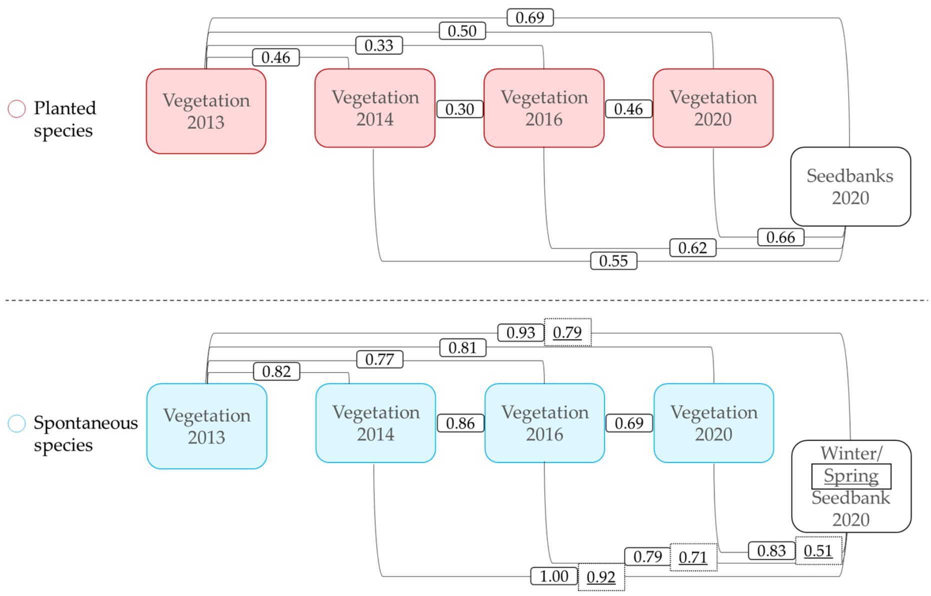

Figure 7. Jaccard index dissimilarity between vegetation from 2013, 2014, 2016, 2020 and the seed bank in 2020 for planted and spontaneous species on an extensive Mediterranean green roof. For spontaneous species, the first Jaccard index corresponds to the comparison with the winter seed bank and the underlined Jaccard index corresponds to the comparison with the spring seed bank.

The dbRDA results showed a significant correlation between the Bray–Curtis divergence and predictor variables (F-value: 3.70 *). Mean plant height, fine sand percentage, total collembola density, CEC, C:N ratio, and plant total cover were all significant (Table 6).

Table 6. Distance-based redundancy analyses (dbRDA) testing for effects of predictor variables on divergence in plant community vegetation (based on Bray–Curtis distance) on an extensive Mediterranean green roof in 2020. F-values, significance levels of ANOVA-like permutation tests and percentage of variation explained by each environmental variable. * $p < 0.05$, NS not significant.

Variable	F-Value	Explained Variation (%)
Mean plant height	10.9	16.40 *
Fine sand	7.31	11.00 *
Total collembola density	7.13	10.70 *
CEC	5.50	8.28 *
C:N	5.49	8.26 *
Total plant cover	4.44	6.67 *
Viable seed density (winter seed bank)	3.47	5.22 NS
pH	2.91	4.38 NS
Organic Matter	2.82	4.24 NS
Clay	2.81	4.23 NS
Fine silt	2.79	4.19 NS
Total mite density	2.67	4.02 NS
Viable seed density (spring seed bank)	2.40	3.61 NS
Bryophyte cover	2.36	3.55 NS
K_2O	1.50	2.25 NS
Coarse silt	0.91	1.37 NS

4. Discussion

The scientific literature has already increasingly focused on the dynamics of plant communities in extensive green roofs, calling for more integrative (i.e., not only vegetation compartments) and specific studies in harsh environments where limiting factors such as water availability amplify the already known constraints of extensive green roofs encountered under semi-arid and arid climates (i.e., without irrigation and with shallower substrates) [19,43].

In our study, we clearly confirm the hypothesis that substrate and exposure affected all studied compartments to varying degrees and we demonstrate that exposure has significant effects on more parameters than substrate.

In the soil, the species-poor winter or spring seedbanks of planted vegetation resulted from seasonal premature drought conditions that have been measured since 2014 in this area [44], which inhibited the completion of the life cycle of the species (no seed production) and, thus, led to differentiation in both structure and composition between the seed bank and observed soil surface vegetation.

Over the period from 2013 to 2020, a loss of planted species clearly occurred with only some perennials (i.e., *Sedum* spp., *Iris lutescens, Allium sphaerocephalon*) and annuals (i.e., *Erophila verna*, *Lobularia maritima*, *Silene conica*) with short life cycles still present and showing a stable trend. Moreover, the roof was colonized by surrounding spontaneous species as often observed in previous studies [27,45–47] on the same type of extensive green roofs but for temperate climates.

The results emphasized the primary ecological processes on extensive green roofs, prevalent in disrupted ecosystems. These processes encompass dispersal, species interactions, and alterations to the environment due to vegetation and other organisms [46,48,49].

4.1. Effect of Substrate on Physico-Chemical Characteristics of the Soil, Winter, and Spring Seed Banks, Mesofauna and Vegetation in the Medium-Term

After 8 years, substrate depth showed a significant effect on all studied compartments, i.e., (i) physico-chemical characteristics of the soil, (ii) winter and spring seed banks, (iii) mesofauna, and (iv) vegetation but to different extents.

The main effect of the depth of the substrate is likely mediated through water retention. Indeed, Getter and Rowe [26] showed that a 4 cm substrate depth held less moisture content than 7 or 10 cm depths. Moreover, the substrate temperature was found to be higher in the shallower substrate and can thus reach the plant heat-stress threshold [43].

Soil variables were moderately impacted by substrate with only lower retention of fine sands and slightly higher fertility in the dryer substrate (i.e., 5 cm substrate without retention layer), maybe due to a lower water retention and mineral absorption of the plant due to the higher presence and cover of annual species than perennial [26,27].

The spring seed bank was highly affected by substrate depth while the winter seed bank was minimally affected. As for soil parameters, the harsher substrate (5 cm substrate without retention layer) exhibited significant differences with a higher viable seed density and a lower evenness of the spring seed bank. This is correlated with a higher number and diversity of annual species in the soil surface vegetation. Annuals rely heavily on seed production in the late spring to propagate and ensure their survival in the following season in autumn. Thus, they produce more seeds than perennial plants, which allocate resources towards storage structures such as roots, rhizomes, and stems, allowing them to store nutrients and energy for extended periods, even under harsh conditions, or use asexual reproduction as a crucial strategy to propagate, which may divert resources away from seed production [50,51].

The substrate affected plant cover and height through a marginal effect on *Sedum album* and a significant effect on *Sedum acre* covers, as expressed by the highest cover in the 5 cm depth substrate with retention layer compared to the 10 cm depth substrate. Indeed, certain plant species are more suited to thrive in shallow substrate. Research on succulent growth in green roofs has already demonstrated that a substrate depth of approximately 7 cm promotes a greater number of *Sedum* species compared to deeper soils [26,52,53]. Moreover, an increase in soil depth can lead to a decrease in the population of certain succulent species over time because of the competition with taller grass and forbs spontaneous species [52].

Planted vegetation was strongly affected by substrate depth through species richness and abundance. The 5 cm substrate depth without retention layer exhibited a lower species richness and abundance than the 10 cm substrate depth with retention layer. As discussed previously for succulent species, substrate depth is a key factor driving species composition and structure: deeper substrate fosters higher species richness and abundance [27,45,52–55] thanks to a stress reduction by a higher water retention capacity and soil temperature mitigation [26,28,56]. Spontaneous vegetation, mostly composed of annual species, did not respond to substrate depth.

The mesofauna community was influenced by substrate depth primarily for Gamasida, and to a lesser extent for Oribatida and hemiedaphic Collembola. Gamasida, which are known to prey on other mites, were particularly impacted [57,58]. Oribatida mites, Gamasida mites, and Collembola are widely used as indicators of moisture levels in soil [59–61]. Furthermore, Chauvat et al. [62] found that hemiedaphic Collembola, adapted to living in the transitional zone between the surface layer and deeper horizons, were the group most affected by soil properties during ecological succession and are commonly used as indicators of soil disturbance [63].

4.2. Effect of Exposure on Physico-Chemical Characteristics of the Soil, Transient and Permanent Seed Banks, Mesofauna, and Vegetation in the Medium Term

Higher clay content was found in the shade, and exposure significantly affected soil fertility illustrated by the increase of nine chemistry parameters in the shade, such as CEC, P_2O_5, K_2O, MgO, CaO, Na_2O, Total N, organic carbon, and organic matter in our case. This result is likely mediated through an increase in soil water content in the shade, which impacts plant growth and results in a higher plant cover and biomass, leading to a higher return of organic matter to the soil [28,64,65].

Nevertheless, significant differences in fine soil granulometry (clays, fine sand, and coarse sand) between substrate depth and exposure can be only explained by an initial difference in the composition of the substrate mixture when the different plots were installed in 2012.

Sun exposure also increased spring seed bank viable seed density and species richness while evenness was found to be lower in the sun exposure. This is likely due to higher competition in the shade and to the presence of more annual species in the sun exposure that produce more seeds than perennials [50,51]. In the shade, which is characterized by a higher fertility of soil, competition for resources with perennial species plays a key role in determining plant community structure and composition [27,54].

Sun exposure reduced total plant cover and Sedum acre cover while it increased Bryophyte cover, likely due to their ability to retain several times their weight in water, enabling them to sustain their growth for longer periods and in harsher areas than expected [66].

Planted vegetation showed a higher abundance in the sun and concomitantly spontaneous vegetation showed an increase in species richness and abundance. Competition appears to have influenced the structure of the plant community, as evidenced by an increase in cover and a decrease in the number of species, with a few dominant species in the shade, such as *Iris lutescens or Allium sphaerocephalon*. The layer of plant species created by these dominant species likely decreased light, nutrient, and water availability for less competitive species [23,45]. Concerning bryophytes, studies are still scarce, but they demonstrated a good establishment in green roofs under harsh climates thanks to their poikilohydric nature [67].

At least total collembola density was influenced by exposure with a higher density in the sun. This could be explained by a preference of collembola to feed on moss [61,68] or by the moisture conditions at the time of sampling, which were more favourable to a greater development of mosses, which provide a more abundant food resource.

4.3. Interactive Effect of Substrate and Exposure on Physico-Chemical Characteristics of the Soil, Winter and Spring Seed Banks, Mesofauna, and Vegetation in the Medium Term

Fewer compartments were affected by the interactive effects of substrate and exposure: spring seed bank, planted vegetation, and total mite density, indicating stress buffering of substrate depth by exposure and vice versa.

Concerning the spring seed bank, in sun exposure, density increased and evenness decreased as the substrate depth decreased and lost water retention capacity, while in the shade exposure, no difference was found among the substrate. The differential response to exposure in harsher substrates is then likely due to a release of competition for small annual species in sun exposure.

Planted vegetation was strongly affected by the substrate × exposure interaction, which was significant for almost all parameters: the Simpson index, evenness, and abundance. The 5 cm substrate depth in the sun is characterized by a dominant annual species (i.e., *Alyssum alyssoides*) more adapted to harsh conditions. Abundance was higher in the 10 cm substrate in the sun due to a buffering of stress by deeper soil. In the shade and with a deeper substrate, a more mesophilic and nitrophilic ruderal vegetation was present (e.g., *Lactuca seriola, Sonchus* sp.) while in the sun exposure, smaller species and short life cycle annuals were found (e.g., *Poa annua*, *Sagina apetala*).

Total mite density decreased significantly with the decreasing depth of the substrate in the sun while substrate had no effect in the shade emphasizing the bioindicative characteristic of mites to soil conditions and specifically to water retention capacity.

4.4. Implications for Extensive Green Roof Installation, Management, and Sustainability under Mediterranean Climate Conditions

The results from this study illustrate a medium-term perspective of the viability of the planted vegetation in a Mediterranean extensive green roof with selected vegetation [25]. Unlike other *Sedum* species, *Sedum acre* and *Sedum album* are confirmed to be an appropriate choice for extensive green roofs in the Mediterranean region [24] thanks to their capacity to survive under drought conditions. Concerning the seed bank, 33% of the planted species were found in 2020, the six same species for the winter and the spring seedbanks. However, 24 and 14 species, respectively, for the spring and the winter seedbanks have colonized the roof.

Concerning standing plant cover, a total of eight planted species and thirty-three spontaneous species were found in 2020, indicating that 44% of the species were established well and are of interest for green roofs in Mediterranean regions. Such perennial species and short-cycle annual species must be chosen as early drought conditions on the roof prevented other species from finishing their life cycle (see Appendix A, Table A1). The colonizing species were mostly *Papaver argemone*, *Stellaria media*, and *Typha latifolia*, which are common in the areas (green spaces, fallow lands, retention ponds, etc.) surrounding the building as observed previously in other studies [27].

Species richness dynamics over time showed two different trends: an increase for spontaneous species and a decrease followed by a stabilization in planted species. Loss of planted species over time is consistent with several previous studies under other climates [27,45,55,56,69,70] and can be the result of competition with spontaneous species that established continuously in the roof by seed rain from the surrounding vegetation and to the impossibility to planted species to finish their life cycle and to produce new seeds due to early drought [23].

Three species were present only in the soil seed bank, e.g., *Chenopodium album*, *Dactylis glomerata*, and *Typha latifolia*; they are all species easily found in the fallow lands and lawns of the surrounding areas of the green roof, but the conditions of the substrates tested, and probably the competition with the introduced species, did not allow these species to grow in the soil surface vegetation since 2012.

This study allowed us to highlight future research needed in order to improve extensive green roof viability under the Mediterranean climate:

As stress tolerance and competition are two main ecological processes occurring in green roofs, the establishment of nurse plants (i.e., *Sedum* spp.) [71] could benefit other species' plant survival and growth and also mesofauna by buffering drought and temperature stress [55,72].

The selection of adapted species/traits based on the study of analogous habitat (habitat template approach) used in this study allowed the establishment of 44% of the planted species. However, the other species disappeared even in the seed bank, highlighting that conditions of drought are not completely analogous to dry Mediterranean grassland species selected. One direction could be to test very local and harvested populations of these species in order to test if ecotypes could exhibit shorter life cycles similar to those experienced on the roof. On the other hand, the choice of analogous habitats should be deepened as green roofs even if they are near the harvested plant area and exhibit peculiar environment conditions with early drought and harsher conditions due to the building properties and elevation.

Bryophytes were a good asset in our study as they were able to better colonize sunny plots than vascular plants and were correlated with a higher mesofauna density, likely explained by their capacity of water retention [67]. Future research is thus needed on biological crusts, which are complex communities of living organisms, including cyanobacteria, lichens, mosses, fungi, and algae, that grow on the surface of the soil in arid and semi-arid regions. Moreover, these crusts play important ecological roles in stabilizing soil, preventing erosion, promoting nutrient cycling, and facilitating water infiltration [67]. Biological crusts could represent a more adapted habitat template to promote extensive green roof viability and multicompartment diversity thanks to similarity to roofs.

Lastly, our study emphasizes the importance of heterogeneity, which allows for higher species richness establishing in different niches [27,53], compensating for a planted species loss trend generally observed in other studies [55,70].

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Appendix A

Table A1. Presence and absence table of planted (**a**) and spontaneous species (**b**) on an extensive Mediterranean green roof from 2013 to 2020.

(a) Planted species								
	2013	**2014**	**2016**	**2020**	**Spring seed bank**	**Winter seed bank**	**Life cycle**	**Biological form**
Allium sphaerocephalon	1	1	1	1	0	0	Perennial	Geophyte
Alyssum alyssoides	1	0	1	1	0	0	Annual	Therophyte/ Hemicryptophyte
Carduus arvensis	1	0	1	0	0	0	Perennial	Geophyte
Clinopodium acinos	0	0	0	0	0	0	Annual	Therophyte/ Hemicryptophyte
Dianthus superbus	1	0	1	0	0	0	Perennial	Hemicryptophyte/ Geophyte
Erophila verna	0	0	0	1	1	1	Annual	Therophyte
Euphorbia cyparissias	0	1	1	0	0	0	Perennial	Hemicryptophyte/ Geophyte
Helianthemum nummularium	1	0	0	0	0	0	Perennial	Phanérophyte
Iris lutescens	1	1	1	1	0	0	Perennial	Geophyte
Lagurus ovatus	1	1	1	1	1	1	Annual	Therophyte/ Hemicryptophyte
Linum bienne	0	1	1	0	0	0	Biennal	Hemicryptophyte
Lobularia maritima	1	1	1	0	1	1	Perennial	Hemicryptophyte
Petrorhagia prolifera	0	0	0	0	0	0	Annual	Therophyte
Plantago afra	1	1	0	0	0	0	Annual	Therophyte
Sedum acre	1	1	1	1	1	1	Perennial	Chamephyte
Sedum album	1	1	1	1	1	1	Perennial	Chamephyte
Sideritis hyssopifolia	1	0	0	0	0	0	Annual-Perennial	T/H
Silene conica	1	1	1	1	1	1	Annual	Therophyte
(b) Spontaneous species								
	2013	**2014**	**2016**	**2020**	**Spring seed bank**	**Winter seed bank**	**Life cycle**	**Biological form**
Arenaria leptoclados	1	0	1	0	0	0	Annual	Therophyte

Table A1. *Cont.*

Arenaria serpyllifolia	0	0	1	1	1	0	Annual	Therophyte/ Chamephyte
Symphyotrichum subulatum	0	0	1	0	0	0	Annual	Therophyte
Avena barbata	0	1	1	1	0	0	Annual	Therophyte
Anisantha sterilis	0	0	0	1	1	0	Annual	Therophyte
Cardamine hirsuta	0	0	1	1	1	1	Biennal	Therophyte/ Hemicryptophyte
Catapodium rigidum	0	0	0	1	0	0	Annual	Therophyte
Celtis australis	1	0	0	0	0	0	Perennial	Phanérophyte
Centranthus calcitrapa	0	0	0	1	1	0	Annual	Therophyte
Cerastium glomeratum	0	0	1	1	1	1	Annual	Therophyte
Chenopodium album	0	0	0	0	1	0		
Erigeron canadensis	0	0	1	0	0	1	Annual	Therophyte/ Hemicryptophyte
Erigeron sumatrensis	0	0	0	1	1	1	Annual	Therophyte
Crepis bursifolia	0	0	0	1	1	0	Biennal	Hemicryptophyte
Crepis foetida	1	1	1	1	0	0	Annual	Therophyte/ Hemicryptophyte
Crepis sancta	0	0	0	1	0	0		
Crepis vesicaria	1	0	0	1	1	0	Biennal	Hemicryptophyte
Dactylis *glomerata*	0	0	0	0	1	0		
Epilobium hirsutum	1	0	0	0	1	1	Perennial	Hemicryptophyte
Erodium cicutarium	0	0	0	1	0	0	Annual	Therophyte/ Hemicryptophyte
Euphorbia maculata	0	0	1	0	1	1	Annual	Therophyte
Geranium molle	1	1	0	1	1	0	Annual	Therophyte
Hordeum murinum	1	0	0	0	0	0	Annual	Therophyte
Hypochaeris radicata	0	0	0	1	0	0	Perennial	Hemicryptophyte
Lactuca serriola	0	0	1	1	0	0	Biennal	Therophyte/ Hemicryptophyte
Medicago sativa	1	0	0	1	0	0	Perennial	Hemicryptophyte
Minuartia hybrida	1	0	1	0	0	0	Annual	Therophyte
Papaver argemone	1	0	0	0	0	0	Annual	Therophyte
Picris echioides	0	0	0	1	0	0	Annual	Therophyte/ Hemicryptophyte
Poa annua	1	0	1	1	1	0	Annual	Therophyte/ Hemicryptophyte
Poa bulbosa	0	0	0	1	0	0	Perennial	Hemicryptophyte
Populus alba	0	0	0	0	0	1	Perennial	Phanérophyte
Rostraria cristata	0	0	1	0	0	0	Annual	Therophyte
Rumex crispus	1	0	0	0	0	1	Perennial	Hemicryptophyte
Sagina apetala	0	0	1	1	1	1	Annual	Therophyte
Podospermum laciniatum	0	0	0	1	0	0	Biennal	Hemicryptophyte
Sedum sediforme	0	0	0	1	0	0	Perennial	Chamephyte
Senecio vulgaris	0	0	1	1	1	1	Annual	Therophyte/ Hemicryptophyte
Sonchus asper	0	0	0	1	1	0	Annual	Therophyte
Sonchus oleraceus	1	1	1	1	1	0	Annual	Therophyte/ Hemicryptophyte
Sophora japonica	0	0	1	1	0	0	Perennial	Phanérophyte
Stellaria media	0	0	0	1	1	1	Annual	Therophyte/ Chamephyte
Taraxacum officinale	0	0	0	1	1	1	Perennial	Hemicryptophyte
Torilis nodosa	0	0	0	1	0	0	Annual	Therophyte
Trifolium campestre	1	0	1	0	0	0	Annual	Therophyte
Typha latifolia	0	0	0	0	1	1	Perennial	Geophyte/ Hemicryptophyte
Urospermum picroides	0	0	0	1	0	0	Annual	Therophyte
Verbena officinalis	0	0	0	0	0	1	Perennial	Hemicryptophyte/ Therophyte
Veronica arvensis	1	0	1	1	1	0	Annual	Therophyte
Viola arvensis	1	0	0	1	1	0	Annual	Therophyte
Viola tricolor	0	0	1	0	0	0	Annual	Therophyte/ Hemicryptophyte
Vulpia ciliata	0	0	1	1	1	0	Annual	Therophyte

Appendix B. Analysis Protocols for Soil Parameters

All analyses were performed at the Teyssier laboratory.

Soil pH (standard NF ISO 10390) was measured with a pH meter in a water solution (using a soil:water ratio of respectively 1:5). Moisture was measured after drying samples at 105°C for 24 h (ISO 11465:1993 cor 1994). For total carbon (C), total organic carbon (Organic C), total nitrogen (N), and Olsen phosphorus (available phosphorus, P), sieved soil was oven-dried at 40°C for 48 h and ground using a ball-mill (Restch, MM400). Carbon and nitrogen were assessed using a CN elemental analyser (Flash EA 1112, Thermo Electron, Germany) (ISO 10694: 1995 and ISO 13878: 1998, respectively). Organic carbon was also measured with a CN elemental analyser after soil decarbonation by HCl. Olsen phosphorus content was assessed by spectrometric determination of phosphorus soluble in sodium hydrogen carbonate solution (ISO 11263: 1998). Finally, from total carbon and total nitrogen soil content, a carbon:nitrogen ratio was computed.

The Cationic Exchange Capacity (CEC) has been determined according to NF X 31-130 by the Metson method; calcium, magnesium, potassium, and sodium cations were determined by agitation and spectrophotometry according to the NF X 31-108 standard. The particle size distribution of the soil particles was determined by the Robinson pipette method (according to NF X 31-107).

References

1. Grimm, N.B.; Faeth, S.H.; Golubiewski, N.E.; Redman, C.L.; Wu, J.; Bai, X.; Briggs, J.M. Global Change and the Ecology of Cities. *Science* **2008**, *319*, 756–760. [CrossRef]
2. Wu, J. Urban Ecology and Sustainability: The State-of-the-Science and Future Directions. *Landsc. Urban Plan.* **2014**, *125*, 209–221. [CrossRef]
3. Grimm, N.B.; Foster, D.; Groffman, P.; Grove, J.M.; Hopkinson, C.S.; Nadelhoffer, K.J.; Pataki, D.E.; Peters, D.P. The Changing Landscape: Ecosystem Responses to Urbanization and Pollution across Climatic and Societal Gradients. *Front. Ecol. Environ.* **2008**, *6*, 264–272. [CrossRef]
4. Raudsepp-Hearne, C.; Peterson, G.D.; Bennett, E.M. Ecosystem Service Bundles for Analyzing Tradeoffs in Diverse Landscapes. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 5242–5247. [CrossRef] [PubMed]
5. Millennium Ecosystem Assessment (Program) (Ed.) *Ecosystems and Human Well-Being: Synthesis*; Island Press: Washington, DC, USA, 2005; ISBN 978-1-59726-040-4.
6. Frazer, L. Paving Paradise: The Peril of Impervious Surfaces. *Environ. Health Perspect.* **2005**, *113*, A456–A462. [CrossRef] [PubMed]
7. Oberndorfer, E.; Lundholm, J.; Bass, B.; Coffman, R.R.; Doshi, H.; Dunnett, N.; Gaffin, S.; Köhler, M.; Liu, K.K.Y.; Rowe, B. Green Roofs as Urban Ecosystems: Ecological Structures, Functions, and Services. *BioScience* **2007**, *57*, 823–833. [CrossRef]
8. Getter, K.L.; Rowe, D.B. The Role of Extensive Green Roofs in Sustainable Development. *HortScience* **2006**, *41*, 1276–1285. [CrossRef]
9. Schrader, S.; Böning, M. Soil Formation on Green Roofs and Its Contribution to Urban Biodiversity with Emphasis on Collembolans. *Pedobiologia* **2006**, *50*, 347–356. [CrossRef]
10. Hobbs, R.J.; Higgs, E.S.; Hall, C. *Novel Ecosystems: Intervening in the New Ecological World Order*; John Wiley & Sons: Hoboken, NJ, USA, 2013; ISBN 978-1-118-35420-9.
11. De-Ville, S.; Menon, M.; Stovin, V. Temporal Variations in the Potential Hydrological Performance of Extensive Green Roof Systems. *J. Hydrol.* **2018**, *558*, 564–578. [CrossRef]
12. Shao, H.; Kim, G. A Comprehensive Review of Different Types of Green Infrastructure to Mitigate Urban Heat Islands: Progress, Functions, and Benefits. *Land* **2022**, *11*, 1792. [CrossRef]
13. Semeraro, T.; Scarano, A.; Buccolieri, R.; Santino, A.; Aarrevaara, E. Planning of Urban Green Spaces: An Ecological Perspective on Human Benefits. *Land* **2021**, *10*, 105. [CrossRef]
14. Kim, J.; Kang, W. Assessing Green Roof Contributions to Tree Canopy Ecosystem Services and Connectivity in a Highly Urbanized Area. *Land* **2022**, *11*, 1281. [CrossRef]
15. Dvorak, B.; Volder, A. Green Roof Vegetation for North American Ecoregions: A Literature Review. *Landsc. Urban Plan.* **2010**, *96*, 197–213. [CrossRef]
16. Köhler, M.; Keeley, M. The Green Roof Tradition in Germany: The Example of Berlin. In *Green Roofs: Ecological Design and Construction*; Schiffer: New York, NY, USA, 2005; pp. 108–112.
17. Fioretti, R.; Palla, A.; Lanza, L.G.; Principi, P. Green Roof Energy and Water Related Performance in the Mediterranean Climate. *Build. Environ.* **2010**, *45*, 1890–1904. [CrossRef]
18. Kotsiris, G.; Nektarios, P.A.; Ntoulas, N.; Kargas, G. An Adaptive Approach to Intensive Green Roofs in the Mediterranean Climatic Region. *Urban For. Urban Green.* **2013**, *12*, 380–392. [CrossRef]

19. Zakeri, S.M.H.; Mahdiyar, A. The Hindrances to Green Roof Adoption in a Semi-Arid Climate Condition. *Sustainability* **2020**, *12*, 9542. [CrossRef]
20. Benvenuti, S.; Bacci, D. Initial Agronomic Performances of Mediterranean Xerophytes in Simulated Dry Green Roofs. *Urban Ecosyst* **2010**, *13*, 349–363. [CrossRef]
21. Williams, N.S.G.; Rayner, J.P.; Raynor, K.J. Green Roofs for a Wide Brown Land: Opportunities and Barriers for Rooftop Greening in Australia. *Urban For. Urban Green.* **2010**, *9*, 245–251. [CrossRef]
22. Agra, H.; Klein, T.; Vasl, A.; Shalom, H.; Kadas, G.; Blaustein, L. Sedum-Dominated Green-Roofs in a Semi-Arid Region Increase CO_2 Concentrations during the Dry Season. *Sci. Total Environ.* **2017**, *584–585*, 1147–1151. [CrossRef]
23. Vasl, A.; Shalom, H.; Kadas, G.J.; Blaustein, L. Sedum—Annual Plant Interactions on Green Roofs: Facilitation, Competition and Exclusion. *Ecol. Eng.* **2017**, *108*, 318–329. [CrossRef]
24. Nektarios, P.A.; Kokkinou, I.; Ntoulas, N. The Effects of Substrate Depth and Irrigation Regime, on Seeded Sedum Species Grown on Urban Extensive Green Roof Systems under Semi-Arid Mediterranean Climatic Conditions. *J. Environ. Manag.* **2021**, *279*, 111607. [CrossRef] [PubMed]
25. Van Mechelen, C.; Dutoit, T.; Hermy, M. Vegetation Development on Different Extensive Green Roof Types in a Mediterranean and Temperate Maritime Climate. *Ecol. Eng.* **2015**, *82*, 571–582. [CrossRef]
26. Getter, K.L.; Rowe, D.B. Substrate Depth Influences Sedum Plant Community on a Green Roof. *HortScience* **2009**, *44*, 401–407. [CrossRef]
27. Brown, C.; Lundholm, J. Microclimate and Substrate Depth Influence Green Roof Plant Community Dynamics. *Landsc. Urban Plan.* **2015**, *143*, 134–142. [CrossRef]
28. Getter, K.; Rowe, D.; Cregg, B. Solar Radiation Intensity Influences Extensive Green Roof Plant Communities. *Urban For. Urban Green.* **2009**, *8*, 269–281. [CrossRef]
29. Van Mechelen, C.; Dutoit, T.; Hermy, M. Adapting Green Roof Irrigation Practices for a Sustainable Future: A Review. *Sustain. Cities Soc.* **2015**, *19*, 74–90. [CrossRef]
30. Dunnett, N.; Kingsbury, N. *Planting Green Roofs and Living Walls*; Timber Press: Portland, OR, USA, 2008; ISBN 0-88192-911-5.
31. Van Mechelen, C.; Dutoit, T.; Hermy, M. Mediterranean Open Habitat Vegetation Offers Great Potential for Extensive Green Roof Design. *Landsc. Urban Plan.* **2014**, *121*, 81–91. [CrossRef]
32. Van Mechelen, C.; Dutoit, T.; Kattge, J.; Hermy, M. Plant Trait Analysis Delivers an Extensive List of Potential Green Roof Species for Mediterranean France. *Ecol. Eng.* **2014**, *67*, 48–59. [CrossRef]
33. Lundholm, J.T. Green Roofs and Facades: A Habitat Template Approach. *Urban Habitats* **2006**, *4*, 87–101.
34. Thompson, K.; Grime, J.P. Seasonal Variation in the Seed Banks of Herbaceous Species in Ten Contrasting Habitats. *J. Ecol.* **1979**, *67*, 893–921. [CrossRef]
35. Heerdt, G.N.J.T.; Verweij, G.L.; Bekker, R.M.; Bakker, J.P. An Improved Method for Seed-Bank Analysis: Seedling Emergence After Removing the Soil by Sieving. *Funct. Ecol.* **1996**, *10*, 144–151. [CrossRef]
36. Mamarot, J.; Rodriguez, A. *Mauvaises Herbes Des Cultures*, 4th ed.; ACTA Association de Coordination Technique Agricole: Paris, France, 2014; ISBN 978-2-85794-284-9.
37. Pielou, E.C. *An Introduction to Mathematical Ecology*; Wiley-Interscience: Hoboken, NJ, USA, 1969.
38. Macfadyen, A. Improved Funnel-Type Extractors for Soil Arthropods. *J. Anim. Ecol.* **1961**, *30*, 171–184. [CrossRef]
39. Gisin, H. Okologie Und Levensgemenischaften Der Collembolen Im Schweizerischen Exkursionsgebiet Basels. *Rev. Suisse De Zool.* **1943**, *50*, 131–224.
40. Borcard, D.; Gillet, F.; Legendre, P. Unconstrained Ordination. In *Numerical Ecology with R*; Use R; Springer: New York, NY, USA, 2011; pp. 115–151; ISBN 978-1-4419-7975-9.
41. Legendre, P.; Anderson, M.J. Distance-Based Redundancy Analysis: Testing Multispecies Responses in Multifactorial Ecological Experiments. *Ecol. Monogr.* **1999**, *69*, 1–24. [CrossRef]
42. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2020.
43. Reyes, R.; Bustamante, W.; Gironás, J.; Pastén, P.A.; Rojas, V.; Suárez, F.; Vera, S.; Victorero, F.; Bonilla, C.A. Effect of Substrate Depth and Roof Layers on Green Roof Temperature and Water Requirements in a Semi-Arid Climate. *Ecol. Eng.* **2016**, *97*, 624–632. [CrossRef]
44. Chenot, J.; Gaget, E.; Moinardeau, C.; Jaunatre, R.; Buisson, E.; Dutoit, T. Substrate Composition and Depth Affect Soil Moisture Behavior and Plant-Soil Relationship on Mediterranean Extensive Green Roofs. *Water* **2017**, *9*, 817. [CrossRef]
45. Dunnett, N.; Nagase, A.; Hallam, A. The Dynamics of Planted and Colonising Species on a Green Roof over Six Growing Seasons 2001–2006: Influence of Substrate Depth. *Urban Ecosyst.* **2008**, *11*, 373–384. [CrossRef]
46. Sutton, R.; Lambrinos, J. *Green Roof Ecosystems: Summary and Synthesis*; Springer: Berlin/Heidelberg, Germany, 2015; pp. 423–440; ISBN 978-3-319-14982-0.
47. Rivière, L.; Delruelle, A.; Reniers, J.; Boisson, S.; Mahy, G. Disentangling Dynamics of Green Roof Vegetation Analogue to Dry Grassland over 3 Years: Plant and Substrate Response to Microenvironmental Variations. *J. Living Archit.* **2022**, *9*, 1–7.
48. Carlisle, S.; Piana, M. Green Roof Plant Assemblage and Dynamics. In *Green Roof Ecosystems*; Sutton, R.K., Ed.; Ecological Studies; Springer International Publishing: Cham, Switzerland, 2015; pp. 285–310; ISBN 978-3-319-14983-7.

49. Rivière, L.; Sellier, A.; Dutoit, T.; Vidaller, C.; Buisson, E.; Mahy, G. The Contribution of Seedbank to the Green Roof Plant Community Dynamics Analogous to Semi-Natural Grasslands. *Front. Ecol. Evol.* **2023**, *11*, 1152319. [CrossRef]
50. Bazzaz, F.A.; Chiariello, N.R.; Coley, P.D.; Pitelka, L.F. Allocating Resources to Reproduction and Defense: New Assessments of the Costs and Benefits of Allocation Patterns in Plants Are Relating Ecological Roles to Resource Use. *BioScience* **1987**, *37*, 58–67. [CrossRef]
51. Tilman, D.; Wedin, D. Plant Traits and Resource Reduction For Five Grasses Growing on a Nitrogen Gradient. *Ecology* **1991**, *72*, 685–700. [CrossRef]
52. Rowe, D.B.; Getter, K.L.; Durhman, A.K. Effect of Green Roof Media Depth on Crassulacean Plant Succession over Seven Years. *Landsc. Urban Plan.* **2012**, *104*, 310–319. [CrossRef]
53. Heim, A.; Lundholm, J. The Effects of Substrate Depth Heterogeneity on Plant Species Coexistence on an Extensive Green Roof. *Ecol. Eng.* **2014**, *68*, 184–188. [CrossRef]
54. Köhler, M.; Poll, P.H. Long-Term Performance of Selected Old Berlin Greenroofs in Comparison to Younger Extensive Greenroofs in Berlin. *Ecol. Eng.* **2010**, *36*, 722–729. [CrossRef]
55. Thuring, C.E.; Dunnett, N.P. Persistence, Loss and Gain: Characterising Mature Green Roof Vegetation by Functional Composition. *Landsc. Urban Plan.* **2019**, *185*, 228–236. [CrossRef]
56. Thuring, C.E.; Berghage, R.D.; Beattie, D.J. Green Roof Plant Responses to Different Substrate Types and Depths under Various Drought Conditions. *HortTechnology* **2010**, *20*, 395–401. [CrossRef]
57. Koehler, H.H. Predatory Mites (Gamasina, Mesostigmata). *Agric. Ecosyst. Environ.* **1999**, *74*, 395–410. [CrossRef]
58. Koehler, H.H. Mesostigmata (Gamasina, Uropodina), Efficient Predators in Agroecosystems. *Agric. Ecosyst. Environ.* **1997**, *62*, 105–117. [CrossRef]
59. Manu, M.; Băncilă, R.I.; Bîrsan, C.C.; Mountford, O.; Onete, M. Soil Mite Communities (Acari: Mesostigmata) as Indicators of Urban Ecosystems in Bucharest, Romania. *Sci. Rep.* **2021**, *11*, 3794. [CrossRef]
60. Seniczak, A.; Seniczak, S.; Iturrondobeitia, J.C.; Gwiazdowicz, D.J.; Waldon-Rudzionek, B.; Flatberg, K.I.; Bolger, T. Mites (Oribatida and Mesostigmata) and Vegetation as Complementary Bioindicators in Peatlands. *Sci. Total Environ.* **2022**, *851*, 158335. [CrossRef]
61. Sławska, M.; Bruckner, A.; Sławski, M. Edaphic Collembola Assemblages of European Temperate Primeval Forests Gradually Change along a Forest-Type Gradient. *Eur. J. Soil Biol.* **2017**, *80*, 92–101. [CrossRef]
62. Chauvat, M.; Wolters, V.; Dauber, J. Response of Collembolan Communities to Land-Use Change and Grassland Succession. *Ecography* **2007**, *30*, 183–192. [CrossRef]
63. MooRE, J.C.; Snider, R.J.; Robertson, L.S. Effects of Different Management Practices on Collembola and Acarina in Corn Production Systems. I: The Effects of No-Tillage and Atrazine. *Pedobiologia* **1984**, *26*, 143–152. [CrossRef]
64. Kobayashi, T.; Hori, Y.; Nomoto, N. Effects of Trampling and Vegetation Removal on Species Diversity and Micro-Environment under Different Shade Conditions. *J. Veg. Sci.* **1997**, *8*, 873–880. [CrossRef]
65. Williams, K.; Caldwell, M.M.; Richards, J.H. The Influence of Shade and Clouds on Soil Water Potential: The Buffered Behavior of Hydraulic Lift. *Plant Soil* **1993**, *157*, 83–95. [CrossRef]
66. Rixen, C.; Mulder, C.P.H. Improved Water Retention Links High Species Richness with Increased Productivity in Arctic Tundra Moss Communities. *Oecologia* **2005**, *146*, 287–299. [CrossRef]
67. Cruz de Carvalho, R.; Varela, Z.; do Paço, T.A.; Branquinho, C. Selecting Potential Moss Species for Green Roofs in the Mediterranean Basin. *Urban Sci.* **2019**, *3*, 57. [CrossRef]
68. Chahartaghi, M.; Langel, R.; Scheu, S.; Ruess, L. Feeding Guilds in Collembola Based on Nitrogen Stable Isotope Ratios. *Soil Biol. Biochem.* **2005**, *37*, 1718–1725. [CrossRef]
69. Emilsson, T. Vegetation Development on Extensive Vegetated Green Roofs: Influence of Substrate Composition, Establishment Method and Species Mix. *Ecol. Eng.* **2008**, *33*, 265–277. [CrossRef]
70. Schrieke, D.; Lönnqvist, J.; Blecken, G.-T.; Williams, N.S.G.; Farrell, C. Socio-Ecological Dimensions of Spontaneous Plants on Green Roofs. *Front. Sustain. Cities* **2021**, *3*, 777128. [CrossRef]
71. Butler, C.; Orians, C.M. Sedum Cools Soil and Can Improve Neighboring Plant Performance during Water Deficit on a Green Roof. *Ecol. Eng.* **2011**, *37*, 1796–1803. [CrossRef]
72. Aguiar, A.C.; Robinson, S.A.; French, K. Friends with Benefits: The Effects of Vegetative Shading on Plant Survival in a Green Roof Environment. *PLoS ONE* **2019**, *14*, e0225078. [CrossRef] [PubMed]