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Title: Community assembly on extensive green roofs: Effects of dispersal-, abiotic- and biotic filtering on the spontaneous species- and functional diversity

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Conflict of interest statement

The authors declare no conflict of interest.

Abstract:

Questions

Extensive green roofs (EGRs) are novel ecosystems and essential tools in mitigating the negative effects of urbanization. However, the extent to which traditional community assembly insights apply to spontaneous plant and trait diversity and composition on EGRs and novel ecosystems in general is unclear: (1) Is a dispersal filter present because of EGRs' fragmented nature (e.g. roof height, urban environment)? (2) Can we confirm the strong abiotic filtering due to extreme EGR conditions (e.g. limited substrate depth)? (3) Does the presence of the planted vegetation lead to biotic filtering?

Location

The Flanders and Brussels region of Belgium.

Methods

The vegetation of 129 EGRs was sampled during a field campaign. Information on local (e.g. substrate, roof height) and regional characteristics (e.g. connectivity indices) was collected and species traits were collected from multiple databases. All data were used to construct (generalized) linear mixed models that tested the effects of the dispersal-, local abiotic- and local biotic filters on

plant community formation. Redundancy analysis was used to investigate predictor effects on functional composition and null models were constructed to assess trait divergence/convergence.

Results

Our results show that the spontaneous plant species diversity is not affected by their landscape context (dispersal filtering), while their functional composition is. Additionally, the importance of abiotic filtering is confirmed, as substrate depth and exposure have a strong impact on species diversity and decreasing substrate depth negatively impacts functional diversity. Finally, we show that biotic filtering by increased planted species cover leads to trait divergence, changes in functional composition and reduced cover of spontaneous species.

Conclusions

We find that a broad perspective which includes the regional and local biotic and abiotic environment is needed to assess all factors that influence the vegetation on EGRs. As biotic interactions are present, EGRs should not be considered as static systems.

Keywords:

Competition; Connectivity; Functional divergence; Linear mixed models; Novel ecosystem; Plant trait diversity; Spontaneously colonizing species; Urban ecology; Vegetated roof

Abbreviations:

AR – D3 anemochory rank; EGR – Extensive green roof; HLI – median heat load index; PROX – proximity; RH – seed releasing height; SDH – standard deviation in structure height; SM – seed mass; SLI – seed longevity index; SVF – median sky view factor

Introduction

In the past decades, green roofs have seen a steady increase in their application and in scientific attention (see e.g. Sutton, 2015). Since these green roofs usually do not interfere with other urban land uses, they are often considered an important method of re-integrating “nature” into cities (Cook-

Patton & Bauerle 2012). Apart from integrating nature, they also deliver a wide range of ecosystem services which improve the urban environment, such as urban heat island reduction (e.g. Susca et al., 2011), water management (e.g. Mentens et al., 2006), improved roof aesthetics (e.g. Jungels et al., 2013), reduced noise pollution (e.g. Van Renterghem & Botteldooren, 2011) and psychological benefits (e.g. Heerwagen, 2000; Lee et al., 2015).

Especially extensive green roofs (EGRs) are widely applied, as these relatively lightweight roofs with substrate depths up to 20 cm, are easy to construct on both new and existing buildings and require only limited maintenance (Oberndorfer et al. 2007). They are prime examples of novel ecosystems (*sensu* Hobbs et al. 2006), whose abiotic conditions and species composition do not occur in ecosystems under natural conditions. Novel ecosystems can arise from deliberate or inadvertent human agency, but human action is not necessary for their continued existence (Hobbs et al. 2006). For EGRs, the species composition often consists of a relatively small fraction of planted species (ca. 30 % e.g. succulent species), and a large fraction of spontaneous colonizers (ca. 70%) (Lysens 2004; Dunnett et al. 2008; Vanstockem et al. 2018).

As the vegetation on EGRs consists of both initially planted and spontaneously colonizing species growing in a man-made environment, this presents us with a complex and novel ecological reality in which it is unclear if the same ecological processes as in natural environments define community assembly, and thus EGR plant species composition. For natural plant communities, spontaneous community assembly (*sensu* Keddy, 1992) is traditionally expected to be mainly governed by three ‘filters’ (Zobel, 1997). More specifically, the species in the regional species pool need to be able to reach the habitat (dispersal filter) and have to establish and survive the local abiotic environment (abiotic filter) as well as interactions with other species (biotic filter) to be able to successfully become part of the local community. More recently, this filtering has shown to be more directly related to the species functional traits, rather than to their taxonomic identity (Ozinga et al. 2005). For example, species characterized by traits related to high dispersability, such as the production of many and light seeds, will be more likely to pass the dispersal filter (Helsen et al. 2013). In the case of EGRs, one could expect a strong effect of the dispersal filter. As they exclusively present fragmented habitats, the amount of species from the regional pool that will be able to reach the EGRs could be

limited. Additionally, their surroundings often consist of mainly non-vegetated, built environments (e.g. buildings, roads). This strong dispersal filter for EGR habitats would then result in a low number of species, of which most would be characterized by a high dispersal ability (and therefore also specific traits, e.g. low seed mass, wind dispersal potential). The connectivity of urban habitats (and thus a less intense dispersal filter) has indeed been shown to significantly influence plant species diversity in urban grasslands (Hejkal et al. 2017), unmanaged semi-intensive green roofs (Catalano et al. 2016) and arthropod diversity on EGRs (Braaker et al. 2013). Additionally, the roof height has furthermore been shown to impact taxonomic and functional composition of EGRs, although results sometimes differ between species groups (Madre et al. 2014; Gabrych et al. 2016). The addition of this vertical dimension to the dispersal filter is typical for these novel ecosystems and is very rarely found in natural systems. The effects of this new dimension on dispersal filter strength are therefore hard to predict.

The local abiotic environment of EGRs is characterized by highly stressful conditions for plants, due to low water availability and strong desiccating effects of high irradiance, extreme temperatures and wind exposition (Dunnett & Kingsbury 2004). These specific abiotic conditions can have a strong filtering effect that leads to a reduced diversity of plant species (Wilson et al. 1987). At the functional trait level, this is expected to lead to trait convergence and thus reduced functional diversity, as only a limited number of stress-adapted traits remain (Cornwell et al. 2006). Mainly leaf economic traits related to more conservative resource use, such as low SLA and leaf nutrients and high LDMC and leaf lifespan are expected to be filtered in these communities (Wright et al. 2004; Hodgson et al. 2011; Reich 2014). The effect of abiotic factors, such as substrate depth, on species diversity and composition on EGRs is well documented (e.g. Madre et al. 2014; Gabrych et al. 2016; Ksiazek-mikenas et al. 2018).

The presence of both planted and spontaneously colonizing plant species on EGRs provides a complex reality in terms of biotic interactions. Furthermore, a considerable part of the urban species pool consists of non-native species (McKinney 2006). In natural systems, biotic interactions such as competition can lead to a reduced species richness (Diamond 1975). Due to the difference in species pools in comparison with natural systems and the presence of many successful (and potentially

competitive) species in urban areas, this biotic filter may be stronger or act differently in novel ecosystems. A short-term study has confirmed biotic filtering on experimental EGRs by showing that *Sedum* presence can reduce colonizing species abundance (Vasl et al. 2017). However, no interaction with annual species sown at the same time as the *Sedum* species was found. From a functional perspective, strong competition for light could also result in a species composition marked by leaf traits related to fast resource acquisition (e.g. specific leaf area, leaf nitrogen content) (Wright et al. 2004; Reich 2014). On the other hand, increased niche competition could occur in high diversity communities and is expected to lead to trait divergence, and thus increased functional diversity, because coexistence is only possible for species occupying different niches (Grime 2006). On EGRs, these competition effects are likely strongly driven by the planted species, as their earlier establishment will likely result in priority effects (Fukami 2015).

While some parts of these assembly filters have been studied on existing EGRs in the past (e.g. Gabrych et al., 2016; Ksiazek-mikenas et al., 2018; Madre et al., 2014), the scope of these studies was often limited to one or two specific filters and the number of green roofs that were studied was often relatively limited. Here, we collected community composition data for 187 zonal samples on 129 EGRs in Northern Belgium, and explored the effects of the dispersal filter, the local abiotic filter and the local biotic filter on the cover, species diversity, functional diversity and functional composition of the spontaneously colonizing species. Overall, we expect that:

- (1) The dispersal filter has a strong effect on EGR assembly, with the added vertical dimension of the filter and the isolated nature of EGRs leading to reduced species and functional diversity.
- (2) The effect of the abiotic filter is similar to the effect in highly stressful natural communities. The most stressful EGR habitats (e.g. thin substrates, highly exposed) will therefore show low cover, species richness and functional diversity. Functional composition will furthermore be filtered toward more conservative resource use traits.
- (3) The biotic filter is important on roofs with a high cover and/or diversity in planted species. Increased resource competition (e.g. for light) in communities with high cover of planted species could result in reduced species richness of colonizing species, with colonization of

mainly competitive species, which are characterized by more acquisitive plants traits. Higher niche competition in highly diverse (species rich) planted communities, on the other hand, could lead to increased functional diversity, due to niche divergence processes in which only functionally distinct species are able to colonize the community.

Methods

Field sampling

From June to September 2015 and 2016, the vegetation on a total of 129 EGRs was studied in northern Belgium (Fig. 1). Roof zones were delineated visually when present, based on homogeneous shade and stress levels, which were inferred from plant height and vegetation type (see Buckland-Nicks et al., 2016). Zone category 1 was characterized by shaded areas with high moss and plant cover and/or higher structural diversity (e.g. plant height), while zone category 2 was distinguished by moderately dry and/or exposed, with a high cover of succulent plant species. Finally, zone category 3 was marked by dry and/or highly exposed areas and limited vegetation cover. A stratified random sampling design was used to assess species cover in 2 m x 2 m plots in the different zones, using the decimal scale (Londo 1976). The number of plots per zone was proportional to zone size (ca. 1 plot per 40 m²). All plant species were identified (using Boyle et al. 2013)) with the exception of the planted *Sedum hispanicum*+*lydium*+*pallidum* and *S. floriferum*+*hybridum*+*kamtschaticum* complexes. All species were assigned to the non-spontaneous (planted or sown, hereafter referred to as planted) or strictly spontaneous classes based on observations and species lists at the time of EGR construction. Additionally, one mixed 250 mL soil sample for the full substrate depth range was gathered from multiple locations for each zonal sample. All observations on plot level were subsequently averaged for the zonal sample in which they were taken, leading to 187 zonal samples (see Appendix S1 for the vegetation matrix for all zonal samples, consisting of 46 that were classified as zone category 1, 129 as category 2 and 13 as category 3). Species richness (SR) and Shannon

diversity (H') were calculated for the combination of all species and for the planted (SR_{pl} and H'_{pl}) and spontaneous species (SR_{sp} and H'_{sp}) separately. Additionally, cover percentages for planted species ($Cover_{pl}$) and spontaneous species ($Cover_{sp}$) were determined. Note that the total of 187 zonal samples were clustered in 129 EGRs across 79 buildings.

Collection of species traits

Plant species traits were obtained from several databases (Table 1) (Kühn et al. 2004; Kleyer et al. 2008; Kattge et al. 2011; Hintze et al. 2013) and supplemented with estimates based on expert judgement (field observations, related species traits) for some species and complexes. The selection of plant traits was based on their relevance in the different filter processes, their impact on green roof functioning (e.g. Lundholm et al. 2015; Xie et al. 2018), their presence in the LHS scheme (height – seed mass – specific leaf area) of Westoby (1998) and their availability for the majority of the species in this study. The gathered seed-related traits such as seed longevity index, seed mass, D3 anemochory ranking index (related to the seed terminal velocity) and seed releasing height can be of interest for dispersal and connectivity. For abiotic stress and competition related responses, the leaf economics traits LDMC, leaf nitrogen content and SLA were gathered. Finally, plant height was also considered relevant for general competition for light. See Appendix S5 for an overview of plant traits and species and Appendix S2 for a full list of references.

Predictors of plant community composition

Landscape factors

Recent orthophoto imagery (Informatie Vlaanderen 2017) was used to create a digital polygon layer for all studied EGRs and calculate their surface area. Using the soil cover map of Flanders (Informatie Vlaanderen 2012) with a resolution of 1 m x 1 m, land cover types surrounding the EGRs were used to create a matrix (potential source habitat/no potential source habitat) to investigate EGR connectivity. Habitats with a high degree of imperviousness (e.g. buildings, roads), a large influence of water (e.g. marsh, tidal flats) or activities prohibiting spontaneous plant colonization were

considered as being no potential source habitats because of the absence of species that could serve as seed sources. All other land cover types were classified as potential seed and species source habitats (for a complete list see Appendix S3). Subsequently, we used FRAGSTATS v4.2 software (McGarigal et al. 2012) to calculate the mean proximity index (PROX; Gustafson & Parker (1992)) for a 200 m radius. This index of landscape configuration has been applied to green roofs in the past (Braaker et al. 2013) and sums all patch areas divided by their nearest-neighboring patch distance (Gustafson & Parker 1992). Additionally, the standard deviation in height (SDH) of surrounding structures (e.g. buildings, trees) in a 200 m radius around the EGRs was calculated to account for possible (vertical) dispersal barriers and the effect of urban canyons. This index is related to relief energy, which is the relative altitude of landscape elements, and originated in geomorphology (Kaulfuss 1974). EGR height above the soil surface was calculated using the most recent digital elevation model for Flanders (DHMVII, (Informatie Vlaanderen 2014)), subtracting the terrain model from the surface model (both with a 1 m resolution). Furthermore, the surface model was used to calculate the median sky view factor (SVF, e.g. Grimmond et al. 2001). This factor can give an indication of the degree a green roof is enclosed by other (higher) buildings and structures, possibly affecting connectivity and its seed trapping capacity. All spatial variables (roof height, SVF and SDH) were calculated with QGIS (version 2.18.4, Quantum GIS Development Team 2016) for digitization, roof height, SVF and SDH) and ArcGIS Desktop (version 10, ESRI 2011). Apart from roof connectivity, the roof age and roof surface area were also included within the landscape context. The effects of connectivity can be expected to accumulate through time or mainly on larger roofs. The effect of roof age on the vegetation composition has indeed been clearly shown before (Madre et al. 2014; Gabrych et al. 2016), while surface area has been found to affect arthropod community composition of green roofs (Madre et al. 2014).

Abiotic factors

The surface model of the digital elevation model for Flanders (see previous paragraph) was used to calculate the mean heat load index (HLI, McCune & Keon 2002) in QGIS 2.18.4. The heat load index has successfully been used to describe the intensity of solar influx in vegetation (Moeslund et

al. 2013, Van Mechelen et al. 2014). pH_{KCl} , electrical conductivity (EC) and C:N ratio were analyzed for each zonal sample. Substrate pH has been shown to influence EGR plant diversity (Thuring & Dunnett 2014), while EC has been used to characterize the plant productivity-related properties (e.g. water-holding capacity, texture) of EGR substrates in the past (e.g. VanWoert et al., 2005). The C:N ratio, which can indicate nitrogen limitation, was demonstrated to evolve over time on EGR (Köhler & Poll 2010). Substrate samples were dried and sieved over a 2 mm sieve to separate the soil fraction which was subsequently subjected to EC and pH_{KCl} measurements with Hanna Instruments HI 98312 and HI991000 sensors, respectively (International Organization for Standardization 2005). Combustive C:N analysis was performed using a Carlo Erba EA1108 elemental analyzer on 10 mg of re-dried soil after HCl addition. Furthermore, the substrate depth was measured for each roof.

Biotic factors

In addition to the species richness and total cover, we calculated functional diversity, based on the eight selected traits of which plant height, seed mass and seed releasing height were log transformed (Table 1). Functional diversity was quantified as Rao's quadratic entropy (Rao's Q, Rao 1982), i.e. the species abundance weighted sum of the pairwise functional distances between species (Botta-Dukát 2005). This measure of functional diversity combines functional richness and divergence in one index and is not sensitive to the low species numbers observed in several samples (which prohibited calculation of the functional richness and divergence indices *sensu* Villéger et al. (2008)). Furthermore, contrary to other functional diversity indices, the correlation between Rao's Q and SR is generally limited (Botta-Dukát 2005). Rao's Q was calculated separately for the spontaneous species (FD_{sp}) and the planted species (FD_{pl}) using the *FD* package (Laliberté & Legendre 2010) in R version 3.4.3 (R Core Team 2017). Before functional diversity calculations, multivariate imputation with chain equations (MICE, Azur et al. 2011) was used to impute missing trait values (Taugourdeau et al. 2014), using the *mice* package (van Buuren & Groothuis-Oudshoorn 2011) in R version 3.4.3 (R Core Team 2017). Finally, the *FD* package was also used to calculate community weighted mean (CWM) values of all plant traits for the spontaneous species in all zonal samples (see Appendix S9 for the resulting plot x CWM matrix).

Statistical analyses

(Generalized) linear mixed models ((G)LMM) were used to investigate the influence of the different variables related to the dispersal, abiotic and biotic filter (Table 2) on Cover_{sp} , SR_{sp} , H'_{sp} , and FD_{sp} in all zonal samples. Multicollinearity among predictor variables was ruled out by calculating variance inflation factors (cut-off level = 3) (Appendix S6). Additionally, the year of sampling and zone category (1, 2 or 3) were included to account for the sampling design. All covariates were z-transformed to aid model convergence. Random effects were included to account for the dependence between roofs on the same building and zonal samples within the same roof. For species richness (count data) we used a GLMM with a Poisson distribution and an observation-level random effect (OLRE) was also included to correct for overdispersion (Harrison 2014). A normal LMM was used for all other models. Backward selection based on AIC was applied (cf. Zuur et al. 2009) and model assumptions were checked for all statistical models. All analyses were performed in R version 3.4.3 (R Core Team 2017), using the *lme4* package (Bates et al. 2014) for (G)LMM. The complete dataset and full model results are presented in Appendices S4 and S7. Additionally, to assess potential trait divergence/convergence patterns at the functional diversity level for the spontaneous species, we constructed a null model for Rao's Q, by randomizing species' abundances within each sample across all species ('richness' randomization) 1000 times in the *picante* R package (Kembel et al. 2010). Rao's Q was subsequently calculated for all within-sample randomized communities to generate a null distribution with which the observed Rao's Q was compared. Trait divergence or convergence is then expected if the observed Rao's Q is, respectively higher or lower, than the generated null distribution (Botta-Dukát & Czúcz 2016; Götzenberger et al. 2016). Finally, a redundancy analysis was performed on the CWM trait matrix (CWM-RDA) and an environmental matrix containing all predictors in Table 2 using the *vegan* package (Oksanen et al. 2017) in R, following the protocol of Kleyer et al. (2012). Subsequently, forward selection based on AIC was applied to reduce the number of predictors and a permutation test was performed to investigate the marginal effects of all predictors in the final RDA (999 permutations). Additionally, *vegan* was also used to perform variation partitioning for the final RDA and determine the importance of the three filters.

Results

The GLMM results show a positive effect of substrate depth and EC on SR_{sp} (Table 3). Furthermore, SR_{sp} decreased with increasing median SVF. For the SR_{sp} model, 27% of the total variation was explained by the fixed effects (R^2_{marginal}), increasing to 55% including the random effects ($R^2_{\text{conditional}}$).

Similar results are found for H'_{sp} (Table 3), for which a positive substrate depth effect and a negative SVF effect are shown. In comparison to the species richness model, a lower percentage of variation is explained by the fixed effects (10%) and fixed and random effects (19%).

For $Cover_{sp}$ (Table 3), while the $Cover_{pl}$ had a negative impact, zonal samples with a higher EC had a higher cover percentage. Higher $Cover_{sp}$ was also found in zonal samples studied in 2016. Finally, $Cover_{sp}$ was negatively affected by median SVF. Of the 41% of variation explained by random and fixed effects, 39% was explained by fixed effects.

Finally, FD_{sp} (Rao's Q) (Table 3) was positively affected by substrate depth and $Cover_{pl}$. The marginal R^2 for this model was 15%, with random effects not causing an increase in explained variation.

Null model results indicate significant trait divergence for ca. 53.9 % of the zonal samples, mainly for samples with FD_{sp} values higher than 5 (Appendix S8.A). Furthermore, a saturation of FD_{sp} can be noticed at high SR_{sp} for simulated values, but is not present for observed FD_{sp} values (Appendix S8.B).

Finally, RDA axes 1 and 2 explained 8.4 % and 2.2 % of the variation in the trait matrix for the final RDA, respectively, with the retained predictors explaining 10.4 % of trait variation (adjusted R^2). The functional composition was significantly structured by $Cover_{pl}$, roof age, roof surface area, PROX, roof height and the median SVF (Table 4, Fig. 2). Variance partitioning indicated that biotic effects ($Cover_{pl}$) explained 2.7 % of trait variance, abiotic effects (SVF, see discussion for the reason of movement from landscape context to abiotic) explained 2.7 % and 5.9 % was explained by the landscape context (PROX, roof age and surface area, roof height).

Discussion

Landscape factors structure composition but do not predict cover or diversity

Contrary to our expectations, landscape variables did not affect spontaneous plant cover and (functional) diversity on EGRs. As the species pool of these roofs is mostly limited to long-distance wind dispersers (CWM anemochory rank = 0.74) this could suggest that the dispersal filter is so strong, that only long-distance dispersers are able to colonize EGR's. This might result in a species pool that is no longer susceptible to small changes in connectivity, thus explaining the absence of dispersal filter effects in our models.

Functional composition was indeed found to be most strongly structured by the landscape context. and a high proximity resulted in a higher proportion of species with high dispersal capacity related traits (height, seed releasing height, anemochory rank). Madre et al. (2014), on the other hand, found no effects of roof height or connectivity on functional composition. The negative effects of connectivity (high proximity, low roof height) on leaf nitrogen and SLA are harder to explain, however. Perhaps these leaf economics effects (*sensu* Wright et al. 2004) are due to the fact that a portion of the good dispersers are tree species (large height, large seed releasing height).

No significant effect of roof age was found for species (functional) diversity or cover, nonetheless supporting earlier studies (Madre et al. 2014; Ksiazek-Mikenas et al. 2018). Plant community functional composition on the other hand, was structured by age in our study, which is again in agreement with earlier studies (Madre et al. 2014; Gabrych et al. 2016). This community composition change resulted in an increase in species with persistent seeds and thus the buildup of a persistent seed bank with age. Furthermore, roof surface area did also not affect diversity patterns but did impact functional composition, again indicating a discrepancy between the effect on composition and diversity measures, which was also observed in Madre et al. (2014).

The negative effect of the sky view factor on SR_{sp} and H'_{sp} was unexpected. We argue that this may be due to a stronger correlation of the sky view factor with increased abiotic stress conditions (e.g. drought, heat, frost), rather than with seed trapping capacity, leading to reduced colonization and species growth (cf. Getter et al. 2009; Piana & Carlisle 2014; Brown & Lundholm 2015). This is further supported by the reduced cover of spontaneous species under high sky view factor, as one could expect that local climatic conditions are more relevant for species growth, than seed influx. Within this abiotic context, the RDA results show that sky view factor leads to higher seed persistence and lower seed mass, both suggesting that stressful environments favor temporal bet-hedging species. The importance of soil seed banks for vegetation composition, has not only been shown for EGR's (Vanstockem et al. 2018), but also for urban wastelands (Albrecht et al. 2011).

Abiotic factors influence diversity and cover

The abiotic EGR characteristics are the main factors influencing the spontaneous species richness and diversity. Similar strong abiotic filtering has been found for other highly stressed ecosystems, such as semi-arid steppe in Spain (Luzuriaga et al. 2012). Even for a small range of substrate depths (ca. 4 to 8 cm in this study), we find a positive effect of depth on species diversity, which agrees with other studies (e.g. Madre et al. 2014; Rowe et al. 2012). Together with the positive effect of the EC on SR_{sp} , it shows that a deeper and more fertile substrate (low stress) will allow for a larger number of species to successfully colonize EGRs (cf. Durhman et al. 2007). Finally, abiotic characteristics influence spontaneous species cover, as indicated by the results for roof exposition (sky view factor, see previous section) and EC on $Cover_{sp}$. Functional diversity was only (positively) affected by substrate depth, suggesting increased abiotic filtering on shallow substrates. Contrary to our expectation and the literature (Madre et al. 2014; Gabrych et al. 2016), abiotic effects only showed a limited effect on the functional composition. Furthermore, only sky view factor was included in the final RDA (see previous paragraph).

Biotic factors affect cover and functional diversity

For the taxon-based diversity measures (SR_{sp} and H'_{sp}) no significant effect of competition is found, even though we see a negative effect of the cover of planted species on the cover of colonizing species, possibly through direct competition for light. Vasl et al. (2017) also showed a reduction in colonizer abundance due to *Sedum* species. Butler & Oriens (2011), on the other hand, reported a facilitating effect for species planted together in an experimental setup. However, most of the colonizer species in our study were ruderals. These species often depend on full light conditions and are hence unlikely to experience facilitating effects of planted species. High cover of planted species furthermore affected functional composition in colonizing species, resulting in increased leaf nitrogen content and SLA, and a decrease in LDMC, as expected, since acquisitive traits become more beneficial when competition for light increases (Reich 2014). Biotic factors furthermore explained about an equal amount of the variation in the functional composition as the abiotic effects.

At the functional diversity level, the null model furthermore indicated clear trait divergence for all plots with high functional diversity ($FD_{sp} > 5$). The positive effect of $Cover_{pl}$ on FD_{sp} thus suggests that niche competition becomes more important in high cover communities, resulting in trait divergence among colonizing species. While this trait divergence has not been reported for green roofs, it has been shown in experimental grasslands (Mason et al. 2011). Abiotic heterogeneity could however be an alternative explanation for the observed trait divergence for the high diversity plots.

Species richness and functional diversity of planted species did not affect the spontaneous vegetation. However, as the planted vegetation mainly contains *Sedum* species, FD_{pl} (median 0.06) is quite low in comparison to FD_{sp} (median 4.30) and may explain why cover was more important than (functional) diversity in affecting assembly patterns.

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Authors' contributions

MH, BS, KH and JV conceived the study and methodology. JV and AB performed field sampling and lab analyses. JV and KH performed data analysis and JV wrote the manuscript with input from MH, BS, KH and AB.

Data accessibility

All data used in this study are included in Appendix S1 (vegetation matrix), Appendix S4 (vegetation and environmental data for model input) and Appendix S9 (trait CWM x plot matrix).

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Tables with legends

Table 1. List of plant traits and the databases from which they were collected. ¹: Kleyer et al. (2008), ²: Hintze et al. (2013), ³: Kattge et al. (2011) + List Appendix S2

Characteristic	Database
<i>Seed longevity index (SLI)</i>	LEDA ¹
<i>Average seed mass (SM)</i>	LEDA ¹
<i>Seed releasing height (RH)</i>	LEDA ¹
<i>D3 anemochory ranking index (AR)</i>	D3 ²
<i>Leaf Dry Matter Content (LDMC)</i>	TRY ³
<i>Leaf nitrogen content per leaf dry mass (LeafN)</i>	TRY ³
<i>Specific leaf area (SLA)</i>	TRY ³
<i>Plant height</i>	TRY ³

Table 2. Overview of all predictors included in the full models, organized by assembly filter. Variables in *italics* collected at zonal level, others at roof level. Note: full models also included year of sampling and zone category.

Landscape factors	Median (min - max)	Local abiotic factors	Median (min - max)	Local biotic factors	Median (min - max)
Roof height (m)	4.56 (1.36 - 25.93)	Substrate depth (cm)	5 (2 - 15)	<i>Cover_{pl}</i> (%)	30 (0 - 113.50)
Standard deviation in structure height (200 m) (SDH) (m)	6.89 (2.91 - 14.98)	<i>pH_{KCl}</i>	6.47 (4.82 - 7.73)	<i>SR_{pl}</i>	5 (0 - 12)
Mean Proximity (200 m) (PROX)	59.63 (0 - 810.92)	<i>Electrical conductivity (EC) (mS)</i>	0.09 (0.03 - 0.73)	<i>FD_{pl}</i>	0.06 (0 - 0.47)
Median Sky view factor (SVF)	0.78 (0.16 - 0.99)	<i>C:N ratio</i>	16.43 (7.8 - 33.94)		
Roof age (years)	6 (0 - 19)	Median Heat load index (HLI)	0.84 (0.23 - 0.85)		
Roof surface area (m ²) (log in analysis)	150 (6 - 2500)				

Table 3. Summary of the final (generalized) linear mixed models results (N = 131) for species richness (SR_{sp}), Shannon diversity (H'_{sp}), cover percentage ($Cover_{sp}$) and functional diversity (FD_{sp}) of spontaneous species.. Beta coefficients (intercept values for categorical variables, slope values for continuous variables) and F statistics are given for each parameter. /: predictor not retained in the final model.

Predictor (Beta (F))	SR_{sp}	H'_{sp}	$Cover_{sp}$	FD_{sp}
(Intercept)	1.74 ***	1.45***	-2.39	5.6 ***
Year of sampling:	/	/	(22.90) ***	(14.68)***
2015			-2.39	5.6
2016			14.7	3.51
Zone category:	(9.32) ***	/	(10.20) ***	/
1	2.18		12.47	
2	1.74		-2.39	
3	1.65		-3.02	
Landscape factors				
Median SVF	-0.21 (15.21) ***	-0.16 (6.14) *	-3.61 (5.98) *	/
Abiotic factors				
Substrate depth	0.21 (11.02) ***	0.17 (6.17) *	/	0.78 (11.18)**
EC	0.15 (5.52) **	/	5.46 (12.41) ***	/
Biotic factors				
Cover _{pl}	/	/	-9.21 (32.21) ***	0.56 (5.32)*
R²_{marginal} (R²_{conditional})	0.27 (0.55)	0.10 (0.19)	0.39 (0.41)	0.14 (0.14)

Significance levels: * p < 0.05; ** p < 0.01; *** p < 0.001

Table 4. Results of the final CWM-RDA model for the spontaneously colonizing species. Degrees of freedom (Df), variance (Var), F-statistic and significance level provided for each variable based on 999 permutations.

Marginal effects	Df	Var	F
PROX	1	0.17	3.19 **
Roof height	1	0.11	2.14 *
Surface area (log)	1	0.16	3.07 **
Age	1	0.16	2.94 *
SVF	1	0.25	4.75 *
Cover _{pl}	1	0.26	4.89 (*)
Residual	124	6.58	

Significance levels: (*) p < 0.10; * p < 0.05; ** p < 0.01; *** p < 0.001

Figures with legends

Fig. 1. Overview of the sampled roofs in Northern Belgium, sampled in 2015 (white) and 2016 (black).

Fig. 2. CWM-RDA plot for the spontaneously colonizing vegetation. Predictors as arrows, in italics. CWM traits as black dots (RH: seed releasing height, LeafN: leaf nitrogen content, SM: seed mass, LDMC: leaf dry matter content, AR: anemochory rank, SLI: seed longevity index, SLA: specific leaf area).

List of appendices

Appendix S1: Vegetation matrix for all 187 zonal samples.

Appendix S2: List of references for trait data gathered from the TRY database.

Appendix S3: Classification and translation of soil cover types into source/non-source habitats.

Appendix S4: Complete dataset containing vegetation and environmental data used in data analysis.

Appendix S5: Species trait summary for all and only spontaneous species.

Appendix S6: Spearman rank correlation matrices containing all explanatory and response variables

Appendix S7: Results of the full (G)LMM models, without backwards selection.

Appendix S8: Null model results for FD_{sp}

Appendix S9: CWM x plot matrix for the spontaneously colonizing vegetation