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Persistence, Loss and Gain: Characterising Mature Green Vegetation by Functional Composition

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Abstract

Like any constructed ecosystem, the vegetation of extensive green roofs (EGRs) will change over time. Although this may influence the desired function and performance, little work has examined the floristic dynamism of EGRs over the long-term. Variations in species composition may be associated with original species (persistent or lost), colonisers (gained), or the effects of spatial heterogeneity. This paper reports on floristic variation of two unmanaged German EGRs twenty years after installation. To evaluate floristic change, the analyses focused on functional composition and plant strategies *sensu* Grime's CSR theory, referring to the basic adaptive strategies of competition, stress-tolerance and ruderality, and their derivatives. With reference to original documentation, less than half the original species persisted. In spite of the losses, both roofs had entire cover, or nearly so, thanks to colonising species. The generalist strategy (CSR strategists) was the most important functional trait in the observed vegetation, followed by stress-tolerance and then by variations in stress-tolerant ruderality. The functional composition of colonising species was chiefly ruderals, followed by stress tolerators and generalists. The drivers behind these changes relate to the pressures of stress, disturbance and competition, as well as spatial heterogeneity and strategies for dispersal and regeneration, seedbank and propagule sources. This study suggests that long-term floristic diversity may be facilitated by ensuring a diversity of traits and species from the start, by providing spatial heterogeneity, and by considering the mechanisms that support persistence and those which determine colonisation.

1. Introduction

Extensive green roofs provide multiple ecosystem services that, like other forms of green infrastructure, help to make cities more liveable and sustainable (Andersson et al., 2015). The projected trend of urbanisation (CBD, 2012, UNFPA, 2007) has obvious implications on the environment and human well-being, and green roofs are recognised tools for mitigating some of the associated problems (Millennium Ecosystem Assessment, 2005). Being shallow (6-15 cm) and lightweight (60-240 kg/m^2), extensive green roofs (EGRs) can retrofit most flat gravel roofs without the need for structural adjustments (Weiler and Scholz-Barth, 2009). Unlike their deeper and heavier counterparts (e.g., semi-extensive and intensive green roofs), EGRs have a high degree of plant cover but require little maintenance. The continued growth of green roof markets (FBB, 2012, Peck, 2014) suggests that these systems will play a role in the ecological matrix of future cities.

The first known study of mature green roof vegetation dates back to Kreh (1945), who listed and categorised all the species that had colonised tar-paper-gravel (TPG) roofs in Stuttgart, Germany. TPG roofs, which involved layers of overlapping tar paper and several centimetres of sand and gravel over a wood deck, were favoured in central Europe in the late 19th century for their ability to inhibit the spread of fire (Arhendt, 2007, Köhler and Poll, 2010). The spontaneous vegetation that colonised these roofs later attracted botanists and ecologists, who applied the methods of phytosociology (Braun-Blanquet, 1972) to classify the vegetation into plant communities (Bornkamm, 1961, Darius and Drepper, 1985, Bossler and Suszka, 1988, Thommen, 1988). This basic query, about how to classify and manage designed ecosystems that have established and become self-regulating with minimal human intervention, has since been re-articulated with the concept of novel ecosystems (Hobbs et al., 2013, Hobbs et al., 2014, Higgs, 2017).

Vegetation composition has consequences for green roof performance (Lundholm and Williams, 2015, Lundholm, 2015). In terrestrial ecosystems, the number and kinds of species present, and the traits they express, influence ecosystem processes like energy and material fluxes, or the alteration of abiotic conditions that regulate process rates (Chapin et al., 2000). On green roofs, planting diverse growth forms (e.g., succulents, tall forbs, dwarf shrubs, creeping forbs, graminoids) can enhance economically valuable services like thermal regulation, substrate cooling, and stormwater retention (Lundholm et al., 2010, Lundholm, 2015, Dunnett et al., 2008a, Nagase and Dunnett, 2012), as well as nitrogen retention (Johnson et al., 2016) and air temperature cooling (Blanusa et al., 2013, MacIvor et al., 2016). The inclusion of broad-leaved plants in a mix, which bear structural qualities that intercept rainfall better than other growth forms, can significantly affect the amount of water retained and released from a green roof (Dunnett et al., 2008a). Similarly, interactions between substrate, moisture, microclimate and different rooting types can critically influence stormwater retention and thermal performance over time (Stovin et al., 2015, Buckland-Nicks et al., 2016). The incorporation of functional diversity and varied growth forms can improve the resilience and performance of green roof systems over the long term (Heim and Lundholm, 2014).

Allocating functional traits to species can grant perspective for understanding vegetation dynamics, since grouping by traits describes the functional character of a plant community at given times and can subsequently serve for comparison (Dunnett et al., 1998, Dunnett and Willis, 2000, Catalano et al., 2016). The pressures of competition, stress and disturbance that are central to CSR theory (Grime, 1974, Grime, 1977) are obvious on green roofs, and the functional traits associated with this have been used for selecting suitable species (Nagase and Dunnett, 2010, Lundholm et al., 2010, Van Mechelen et al., 2014). According to CSR theory, natural selection pressures have led to the evolution of adaptive life strategies conforming to distinct habitat types, whereby competitors (C) exploit conditions of low stress and low disturbance; stress-tolerators (S) exploit high stress, low disturbance habitats; and ruderals (R) benefit from low stress, high-disturbance situations (Grime, 2001). In addition to these primary strategies, the theory proposes that intermediate intensities of these pressures have led to secondary strategies; those relevant to green roofs include competitive ruderals (CR), which are adapted to circumstances with low stress where competition is restricted to a moderate intensity by disturbance; stress-tolerant ruderals (SR), which are adapted to lightly-disturbed, unproductive habitats; stress-tolerant competitors (SC), which are adapted to relatively undisturbed conditions that experience moderate intensities of stress; and 'CSR strategists' , which are adapted to habitats in which competition is restricted by moderate intensities of both stress and disturbance (Grime, 2001).

After twenty or thirty years, the functional diversity of shallow green roof vegetation appears to shift more towards cover by ruderals and stress-tolerators and fewer competitive species (Köhler, 2006, Catalano et al., 2016). Stress tolerators, such as sedums, can maximise limited resources while ruderal species, such as annual grasses, can maximise resources in disturbed conditions and either avoid destruction or recover rapidly (Dunnett, 2015). Twenty years of biannual surveys on two EGRs in Berlin revealed fluctuations in species diversity whereby wet summer periods led to enhanced diversity through colonising annual species, and the discontinuation of irrigation led to dominance by a few species (Köhler, 2006). In that study, the roof installed with a pre-cultivated mat became dominated by Chives, while the roof with a conventional build-up became dominated by Sedums and not a single Chive (*ibid*). In Hannover, an early decrease in competitors and an increase in ruderals and stress-tolerators was reported for a sample of fifteen simple-intensive turf roofs based by topsoil and light aggregates (Catalano et al., 2016). These two studies suggest that turf mats may promote certain species and discourage others through the productivity and propagule store of the topsoil and associated barriers to colonisation. With respect to typical EGRs, the few studies that have examined long-term vegetation development have not considered functional composition but rather growth forms based on bud location (Thommen, 1988, Buttschardt, 2001, Poll, 2008) or species diversity and abundance (Thuring and Dunnett, 2014, Köhler, 2006, Köhler and Poll, 2010).

Long-term observations of ecological phenomena and biodiversity, and the consistent and reliable accumulation of long-term synoptic datasets, are crucial to understanding how natural systems work (Callahan, 1984, Likens, 1989, Franklin et al., 1990), and for addressing questions on causation ("why") and mechanisms ("how") (Bakker et al., 1996). Long-term observations of green roofs are useful for planning guidance (Rowe et al., 2012), especially since studies that have observed green roof vegetation continuously over several years report that conclusions drawn from later observations differ from those drawn after one or two growing seasons (Getter et al., 2009, Köhler, 2006, Köhler and Poll, 2010, Lundholm et al., 2010, Catalano et al., 2016, Rowe et al., 2012). The FLL guideline (2008), which is designed to ensure quality and function for all green roof types, emphasises installation and early establishment period but does not allude to long-term performance or diversity.

This study examines the vegetation of two EGRs twenty years after installation in Stuttgart, Germany. Our objective was to characterise changes in mature green roof vegetation with reference to functional types using CSR theory. With respect to the roofs surveyed, we inquired into the relationship between original species (persistence and loss) and colonisers (gain). How does the functional character of today's vegetation relate to that of original lists? Did EGR vegetation converge over time, eventually expressing comparable properties, functional types and composition regardless of initial lists? Or did it diverge such that each roof supported a unique flora dictated by site-specific factors and conditions?

We hypothesised that the functional composition and species assemblage on unmanaged extensive green roofs will have changed after two decades. Specific aims were: (1) to establish the proportion of functional types and the species that persisted, disappeared, or colonised; (2) to determine changes in diversity of over time; and (3) to identify the conditions and factors that influence vegetation dynamics on EGRs.

2. Methods

2.1. Study area

The study area involved two extensive green roofs in Stuttgart (Germany, 48°47' N, 9°10' E; 252 m a.s.l.) (**Figure 1**). According to the Köppen-Geiger Climate Classification, Stuttgart has a warm-temperate climate, with "fully humid" precipitation rates, warm summers and no dry season (Kottek et al., 2006). Most of its annual rainfall (annual average: 689 mm) occurs in the summer months (highest average in June: 96 mm) (DWD Climate Data Centre, 2016).

Figure 1. The study area was in and around Stuttgart in south-west Germany (Google Maps, 2018).

The roofs were constructed in 1990 and 1991 using three-layered constructions typical of extensive green roofs (as per FLL guidelines), although no system manufacturers were listed, and installed with 80-100 mm evenly distributed green roof substrate. The documentation received from building owners included green roof specifications (Rathausgarage), and correspondence records from the architect along with specifications and relevant drawings (Killesberg). Both roofs were sown with wildflower seed and *Sedum* cuttings, and the species lists were very similar (**Table 1).**

The first site, **Rathausgarage complex**, was a multi-story parking garage for Stuttgart Town Hall that was sown with seed and Sedum cuttings in spring/ summer 1990. Of the two sub-roofs, “Rathaus PV” (1,300 m^2) featured a row of solar panels at its south-west corner, and “Rathaus lower” (1,100 m^2) adjoined the PV roof a meter lower (**Figure 2a**). From 1991 until 2008 the roofs were maintained once annually in the form of weeding and clearing drains; by the time of sampling they had been unmaintained for three years (Heller, 2011). The second site, **Killesberg** (450 m^2), had an inclination of 30° with distinct North-South aspects (**Figure 2b**). The site was originally built for demonstration and served as headquarters for the International Garden Show in 1991, after which the Department of Gardens, Cemeteries and Forests took occupancy.

Figure 2. The roofs surveyed in Stuttgart included a) Rathausgarage complex and b) Killesberg.

2.2. Vegetation data

The roofs were sampled with 1 m^2 plots using sampling methods appropriate to the site, taking care to ensure representative vegetation by avoiding edges and mounds (Braun-Blanquet, 1932, Mueller-Dombois and Ellenberg, 1974, van der Maarel, 2005, Rodwell, 2006). A stratified random approach was taken at the Rathausgarage complex, whereby non-uniform patches were defined first (e.g., shrubby mounds) after which the dominant vegetation was sampled through the random placement of quadrats within the designated area. On the pitched roof at Killesberg, five randomly chosen points along the ridge served for the placement of transects, along which sampling quadrats were then randomly placed. Stratifying, or dividing, vegetation into homogeneous (uniform) versus heterogeneous (non-uniform) patches prior to placing samples is beneficial for clustering major sources of variation (van der Maarel, 2005).

Vegetation surveys were conducted over one growing season, from early-June to mid-July in 2011, with percentage cover (%) recorded per species and growth form. Eighteen quadrats were sampled on Killesberg, fourteen on Rathaus lower, and fifteen on Rathaus PV. The methods for vegetation sampling and description followed the National Vegetation Classification Users' handbook (2006). Taxonomic nomenclature was standardised using The Plant List (http://www.theplantlist.org/, accessed in November 2015). If species from original lists did not arise in any quadrats, a reconnaissance of the whole roof was conducted in order to confirm whether they had been fully extirpated, or simply did not appear in the quadrats. All species were labelled with functional traits drawn from the BiolFlor online database (Klotz et al., 2002), which describe adaptive strategies using CSR traits.

2.3. Data analysis

Original species lists were used to determine which species had persisted, disappeared or colonised per roof. Consequently, the observed vegetation from our surveys included the original (i.e., persistent) and colonising (i.e., gained) species that were identified per quadrat; original species that were not found were considered lost. Since composition and cover by original species were not explicitly known, the functional character for the original vegetation was established hypothetically by assuming a total cover value of 100% for each roof and therewith allocating the species of original lists with equal cover values that totalled 100%. Though the functional composition resulting from this method may differ from the actual vegetation that established initially, this metric was deemed sufficiently general yet informative for the purposes of this analysis.

The analysis therefore begins by assessing the species cover and functional composition of individual roofs, and then expands to consider the total cover of observed vegetation from all the quadrats sampled. In order to describe proportionate cover by each species and each functional type, proportionate values were calculated with reference to the total cover of all species per respective sample, whether per roof or both. Wilcoxan Signed Rank Tests were conducted to determine whether the functional composition of species had shifted significantly between initial and observed time periods (IBMCorp., 2011).

Next, the comparison of plant community composition between original lists and observed vegetation was achieved using Baycentric plots comprising three variables. To this end, the data was recalculated into a matrix of CSR signatures for each quadrat from both roofs. In order to illustrate the effect of the North-South gradient at Killesberg, the same process was applied to that data but distinguishing and grouping the quadrats accordingly. All data processing and analysis was performed using R software (version 3.4.2) (R Core Team, 2017) and R package ‘tidyverse’ (version 2.1.1) (Wickham, 2017). Ternary diagrams were constructed using ggtern (R package version 2.2.1) (Hamilton, 2017).

3. Results

3.1. Vegetation change

Overall, less than half the species from original lists persisted after twenty years, with 36.4% persisting at Killesberg (i.e., 63.7% lost) and 44% persisting at the Rathausgarage complex (i.e., 55.9% lost) (**Table 2**). Similar analyses of the sub-roofs at Rathausgarage also indicate low cover by persistent species (below 45%) and higher rates of disappearance (upwards of 55%). Although many of the initial species had disappeared, species diversity was bolstered with around 60% cover by spontaneous colonisers. In order to elucidate the causes and mechanisms of these changes, and to establish the effectiveness of original lists, the ecological strategies of the species that persisted, disappeared, and colonised were examined more closely with consideration of proportionate cover across all roofs and absolute cover on individual roofs.

3.1.1. Original species: persistent vs. lost

The species that had persisted twenty years after installation were represented by a variety of functional types, the majority being CSR strategists followed by stress-tolerators, stress-tolerant competitors, and single individuals of C, R, and SR strategists. The CSR strategists included frequently used green roof plants (*Allium flavum, Dianthus carthusianorum, D. deltoides, Festuca ovina, Hieracium pilosella, Poa compressa, Thymus serpyllum, T. pulegioides*), of which some occurred very sparsely or had disappeared on at least one of the roofs (*Dianthus deltoides*, *Campanula rotundifolia*). The stress-tolerators were all *Sedums*, of which some had high cover (*S. rupestre, S. hybridum, S. sexangulare*) while others were scarce (*S. acre*). One of the stress-tolerant competitors (SC), *Linum perenne*, was abundant on all the roofs, while the others were infrequent (*Potentilla argentea,* *Sedum telephium, Veronica spicata*). The SR strategist, *Trifolium arvense*, only occurred on Killesberg, in 30% of quadrats.

When re-calculating the percent cover of individual species proportionate to the total cover recorded by all species, stress-tolerators became the predominant functional type (50%). Nine of the S-strategists were *Sedum* taxa, one was *Sempervivum*, and the remainder were bryophytes. The extensive cover provided by this functional type was granted mainly by five *Sedum* species, championed by *Sedum hybridum* (17.7%) and followed by *S. rupestre* (8.1%), *S. sexangulare* (7.9%), *S. spurium* (5.7%), and *S. kamtschaticum* (5.3%); the remaining S-strategists had under 2% of the total proportionate cover (**Table 3**). While *S. hybridum* and *S. rupestre* did have the greatest presence of all the *Sedum* taxa, the high cover values are also associated with their structure and form. Compared with the fine foliage and small forms of *S. sexangulare* and *S. acre*, for example, *S. rupestre* forms large cushions while *S. hybridum* has large, flat foliage. CSR strategists played an important role to the functional composition of the observed vegetation (28%), but the most successful CSR species, *Festuca ovina*, had the same proportionate cover as the lowest ranking of the top *Sedum species* (5.7%). Small proportions of ruderals (7.8%), stress-tolerant ruderals (7.3%), and less than 3% cover by competitors and stress-tolerant competitors round off the functional character of these roofs. The negligible cover by competitive ruderals (0.04%) is owing to single individuals of *Erigeron annuus*, *Cerastium arvense*, and *Convolvulus arvensis*.

With respect to loss, the number of species and associated functional types that disappeared were similar to those that persisted, with the exception that more CSR species were lost (11) than persisted (8). Some of the original species that did not survive on either roof included *Digitaria sanguinalis* (R), *Inula hirta* (SC), *Onobrychis viciifolia* (C), *Plantago major* (CSR), *Poa nemoralis* (CSR), *Polygonum aviculare* (R), *Rumex acetosella* (CSR), and

Saponaria ocymoides (SC). Reconnaissance of the greater roof area, beyond sampling plots, confirmed that these species had been completely extirpated. Surprising losses included common green roof plants, like *Sedum acre* and *S. spurium*. Both are pure S-strategists, yet the former was not evident on any of the roofs surveyed, and only a small individual of *Sedum acre* was found in a single quadrat of the lower Rathaus roof. Although some studies have found *S. acre* to maintain stable cover over 4 to 7 years (Rowe et al., 2012, Bates et al., 2013), here it did not persist after twenty years. The eventual disappearance of these species may relate to their comparatively delicate stature by contrast with larger-leaved species, or to their regenerative strategies of vegetative spread, which are challenged when the green roof achieves a closed canopy with few gaps or bare substrate. Further work is required to substantiate this.

3.1.2. Gained (colonising) species

In addition to the dynamics of persistence and loss, the vegetation of these roofs was bolstered by colonising species that comprised 64% of the observed cover at Killesberg and 54.5% of the observed cover at the Rathaus complex. The majority of colonising species (7 of 25) were stress-tolerant ruderals (SR), of which five were mosses, one an herbaceous annual (*Petrorhagia prolifera*) and one a ruderal grass (*Vulpia myuros*). The next most abundant functional type amongst colonising species was stress-tolerance (6 of 25), half of which were bryophytes, including two lichens and one moss. Three of the stress-tolerant colonisers were *Sedum* that were specified on the Rathaus complex but not on the Killesberg roof. Killesberg was only specified with *Sedum acre*, yet *S. album, S. rupestre* and *S. sexangulare* all had relatively high coverage on that roof and occurred in more than half the quadrats surveyed. Not including those *Sedum* species, colonisers common to both roofs included three bryophytes (*Cladonia scabricula, Peltigera spp.*, the unidentifiable “Starry yellow moss”) and *Vulpia myuros*.

The five colonising CSR strategists included species with abundant cover and occurring in nearly every quadrat (*Crepis tectorum, Potentilla tabernaemontani*), while others were consistent but not as abundant (*Taraxacum officinale*) and some were sparse and sporadic (*Potentilla erecta, Picris hieracioides*). The biennial *Picris* only occurred in a few quadrats on the Rathaus complex, similar to the evergreen rhizomatous *Potentilla erecta*. Just as the fleshy tap-rooted, rosette-forming Dandelion occurred on each roof only as a few individuals with minimal cover, the competitive colonisers (*Acer pseudoplatanus, Carpinus betulus*, *Verbascum nigrum*) also occurred as infrequent individuals. Trees do not seem to persist beyond one year on EGRs, judging from the absence of older specimens, probably due to the limited resources of the shallow substrate and the challenging growing conditions.

3.1.3. Observed vegetation: persistent + gained

Based on total, proportionate cover of the vegetation surveyed on all roofs, the top ten species observed (i.e., persistent and gained species in the surveyed quadrats) comprised nine original persistent species and one coloniser (**Table 4**). Four of the ten species were CSR strategists, including two typical green roof plants, *Festuca ovina* and *Dianthus carthusianorum,* as well as *Hieracium pilosella* and the only coloniser of the top ten, *Crepis tectorum*. The three stress-tolerators included *Sedum rupestre,* which had the greatest cover and highest frequency, as well as *Sedum sexangulare* and *S. hybridum*. The sown ruderal, *Setaria viridis*, occurred on all roofs with consistent, if diminutive, cover. The other top ten species included a stress-tolerator grass (*Vulpia myuros*) and *Linum perenne*, a stress-tolerant competitor (SC). Despite the limitations of the study, these results clearly depict the functional character of the vegetation and suggest that certain traits are advantageous to long-term persistence on EGRs.

The most abundant species, *Sedum rupestre*, occurred in nearly all quadrats on both roofs, and had the highest proportionate cover of all species. With its upright and spreading habit, *S. rupestre* formed an extensive ground cover that was sometimes totally exposed to direct sunlight, and other times shaded beneath taller herbaceous species. The ruderal Green bristle grass (*Setaria viridis*) was very abundant and frequent, but it did not create a visible impression given its dwarfed stature; although it can grow 100-600 mm high (Hubbard, 1992), the *Setaria* on these roofs never exceeded 100 mm (*data not shown*). The CSR coloniser, *Crepis tectorum* occurred in nearly all quadrats on the Rathausgarage complex, and its high cover abundance can be explained by basal rosette leaves. The name of this species implies its affinity for the roof habitat (Archibold and Wagner, 2007). The other CSR strategist, *Festuca ovina*, occurred as consistent tufts but did not occupy more than 10% of total proportionate cover for all roofs. The other species from the top 10 observed cover included three ground-covering Sedums (*S. album, S. hybridum, S. sexangulare*) and two stress-tolerant competitors, *Linum perenne* and *Veronica spicata*.

3.1.4. Functional composition over time

The functional composition of these roofs changed significantly from the time of installation to the surveys of 2011, with medium to large effect sizes according to Cohen (1988). Whereas initial lists featured around 30% competitive species, after twenty years less than 15% of the observed species fell into this category ($z= 3.464$, $p<.001$). Our surveys in 2011 found that stress tolerators had between 50-70% cover, whereas this functional type comprised 30-40% of the original species lists (**Table 5**). With regards to functional character, the initial species list for Rathausgarage classified as SC/CSR, and the surveyed vegetation 20 years later was defined as S/CSR. Similarly, the Killesberg vegetation shifted from S/CSR to S/SR classification (**Figure 3**). Although rudimentary, these results are corroborated by other studies that mature green roof vegetation shifts away from competitive strategies towards a vegetation defined by stress-tolerant and/ or stress-tolerant ruderals

(Catalano et al., 2016, Köhler, 2006) or by CSR generalists such as *Allium schoenoprasum* (Köhler, 2006).

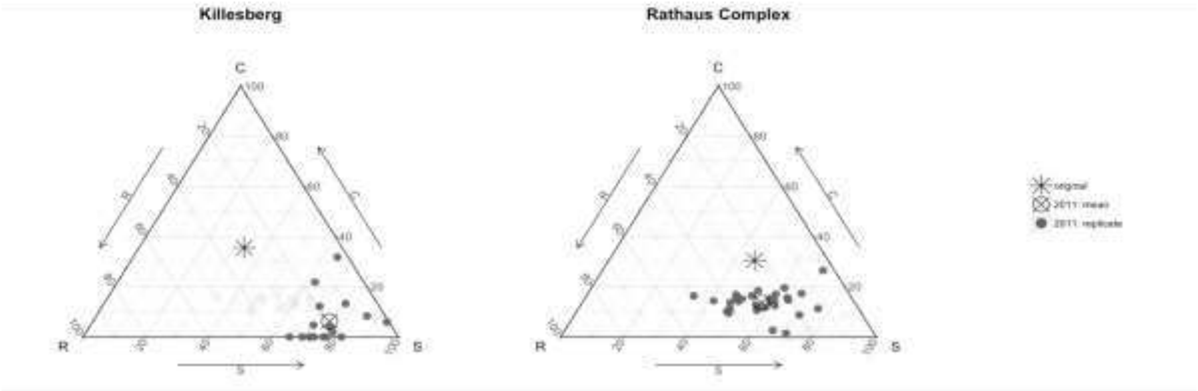

Figure 3. The functional character of the roofs surveyed shifted from SC/CSR and CSR vegetation towards communities defined by S- and SR strategists.

3.2. Effect of heterogeneity and microclimate

The same trend of shifting functional character is evident on the pitched roof at Killesberg, where the distinct North- South- aspects offer an extreme example of the effect that heterogeneity can play on vegetation development. In spite of being sown with the same species, at the same time and onto an identical build-up, the functional composition of the two aspects diverged into distinct characters. The original species list classified as CSR, but by 2011 the vegetation on the North-face was S/CSR while the South-face was S/SR (**Figure 4**). This can be described floristically: the North-facing roof featured a Sedum groundcover beneath a dense meadow of herbaceous vegetation, while the South-face comprised a single-layer of Sedums, stress-tolerant mosses and ruderal grasses, often growing sparsely over bare and cracked substrate.

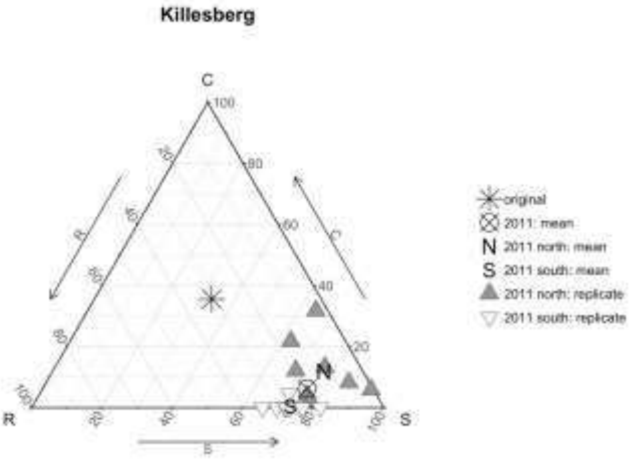

Figure 4. The functional character of the vegetation at Killesberg diverged according to aspect.

Nearly half (43%) the original species were lost on Killesberg, including some that might have been expected to thrive given their rigour in urban environments (*e.g., Digitaria sanguinalis, Plantago major*) or on green roofs (e.g., *Agrostis tenuis, Hieracium pilosella, Poa compressa*). A few Sedum species were observed in relative abundance on both aspects (*S. album, S. rupestre, S. sexangulare*), and the grasses *Festuca ovina* (CSR), *Setaria viridis* (R) and *Vulpia myuros* (R) were present on both aspects but best represented on the North face.

4. Discussion

4.1. Persistence, loss, and gain

A simple analysis of functional traits is unlikely to predict persistence by original species, but it can help to explain long-term species composition. Although the green roofs surveyed were sown with multiple species, the species that persisted, disappeared and colonised all exhibited a variety of adaptive strategies, often in combination. While it is unsurprising that species typical of mesic meadows did not persist on these roofs, neither did several species derived from disturbed wastelands and rocky habitats, including ruderal strategists and stress-tolerators. The majority of ruderal species introduced at the outset may have disappeared due to a lack of regular disturbance, and the ruderals observed twenty years later may have been successful not from having formed persistent populations on the roofs but rather from regular replenishment through dispersal or other mechanisms. Species extirpation from green roofs can perhaps be attributed to effects that our brief surveys could not register, e.g., catastrophic droughts (Rumble and Gange, 2013), spatial environmental heterogeneities (Buckland-Nicks et al., 2016), or inter-specific competition/ facilitation (Heim and Lundholm, 2014, Butler and Orians, 2011).

In recent years, annual species have received growing commendation for their use on green roofs (Van Mechelen et al., 2014, Dunnett, 2015), and our surveys verify that ruderal strategies form an important component of mature EGR vegetation. Colonising plants and mosses fill in gaps created by dead or dying plants, thereby replacing bare ground with vegetative cover, which is essential for green roof ecosystem services (Lundholm, 2015). Seedbank may be an important resource for the maintenance of species diversity on green roofs over time, too (Buttschardt, 2001, Köhler, 2006, Köhler and Poll, 2010, Olly et al., 2011). Given that bare soil, the requirement for colonisation, offers the lowest returns on most ecosystem services and puts the system at risk of erosion, we advocate preventing this incidence by sowing an abundant pool of appropriate species, ensuring establishment, and then welcoming colonisers once the vegetation has established. Future work exploring the dynamics of designed plant communities should compare bare control plots with planted replicates and observe whether the vegetation converges regardless of planting, or to what extent original plantings determine the nature and quality of vegetation development over time.

4.2. Functional characterisation of mature EGR vegetation

Our results confirm that green roof vegetation shifts towards functional composition defined by stress-tolerators and ruderal species (Köhler, 2006, Catalano et al., 2016), but add that competitive and secondary strategies are also important traits. The presence of CSR strategists in the mature vegetation indicates that moderate stress and disturbance pose restrictions on competition, while the SR and SC types imply an even lighter combination of these pressures (Grime, 2001). Long-term persistence in the form of compact, slow growth and vegetative reproduction are hallmarks of the stress tolerator strategy (Grime, 1977), while the ruderal strategy is typified by persistence in the form of either rapid annual or short-lived perennial life cycles, with investment into seed rather than vegetative development (Harper, 1977). Two years after installation, competitive species of fifteen sod roofs in Hannover had decreased while wind-dispersed species had increased, and another ten years on the vegetation had shifted substantially to stress-tolerators whose short -distance dispersal was attributed to ants (Catalano et al., 2016). Ants were observed on all the roofs surveyed here, too. The role of dispersal mechanisms and regenerative strategies will be an important parameter to include in future research on green roof vegetation dynamics.

In addition to successional shifts in functional composition, we inquired whether unmanaged extensive green roof vegetation eventually assumes emergent properties. In other words, does mature roof vegetation on similar constructions come to express consistent characteristics regardless of location, such that the degree of complexity is greater than the effect of individual species (Ponge, 2005)? This question marked the origin of ecological query on vegetated roofs, whereby the methods of phytosociology were applied to over 100 spontaneously vegetated tar-paper gravel roofs in Central Europe (Bornkamm, 1961, Bossler and Suszka, 1988, Darius and Drepper, 1983, Thommen, 1988, Buttschardt, 2001). Although the *Sedo-Scleranthetea* (Br.-B. 55 em. Th. Müller 1961) was classified for nearly all roofs, this is the broadest categorisation on the classification hierarchy with the lowest resolution. Indeed, even the *Poetum anceptis-Poa compressae* association, which was classified explicitly for this roof vegetation type (Bornkamm, 1961), was rarely satisfactorily confirmed because at least one key species would be absent while colonisers were too abundant (Bornkamm, 1961, Darius and Drepper, 1983, Bossler and Suszka, 1988, Thommen, 1988, Buttschardt, 2001). Given the heterogeneity of conditions influencing the urban flora (Hill et al., 2002), it could be that the methods of Braun-Blanquet (1972), or classification in general, are unsuitable for urban habitats. For EGRs, in any case, our surveys suggest that vegetation will most typically diverge into unique assemblages per roof and that convergence would depend on replications of multi-variate factors that may include, but are not limited to, spatial heterogeneity, regenerative strategies, various forms of competition, and stochastic phenomena.

4.3. Role of heterogeneity and microclimate in vegetation development

These observations mirror the results of systematic studies examining EGR vegetation in roof platforms or replicated plots (Rowe et al., 2012; Dunnett et al. 2008), and resonate with the recent suggestion that spatial heterogeneity is a major driver of EGR vegetation cover and growth (Buckland-Nicks et al., 2016). To the suggestion that green roof design should consider microclimate when selecting plant species (Brown and Lundholm, 2015), this study agrees that plant mixes should contain a range of functional types at the outset because small-scale heterogeneity will naturally direct the vegetation towards the best suited assemblages, in dynamic process. In addition, objects casting shade onto the roof, such as neighbouring trees (Köhler, 2006) or roof structures (Buckland-Nicks et al., 2016), may diversify the vegetation whereby shade-loving plants co-exist alongside species of high light environments. So, if increasing functional diversity increases the provision of ecosystem services and multi-functionality on green roofs (Lundholm, 2015, Buckland-Nicks et al., 2016), then bolstering species lists accordingly may serve as a form of best practice, particularly for installations intended for long-term performance.

Controlled studies of plant mixtures on green roofs over time have demonstrated that diversity tends to decline from original composition (Riedmüller, 1994, Buttschardt, 2001, Köhler, 2006, Dunnett et al., 2008b, Lundholm et al., 2010, Schroll et al., 2011, Rowe et al., 2012, Madre et al., 2014), but our surveys of typical EGRs twenty years after installation observed that the number of species that disappeared was replaced in nearly equal measure by colonisers. This opens a point of query with relation to the long-term consideration of species lists as recommended by green roof guidelines, such as the frequently cited FLL (2008) that have been adapted in many other regions of the world, in some cases very closely (e.g., GRO, 2014). If EGR vegetation is now known to change quite dramatically over time, such that mature roofs comprise more colonisers than original species, how is this information most appropriately shared amongst practitioners and designers? Do guidelines that are focused on establishment obscure long-term perspective and opportunities for biodiversity? If EGRs are treated as designed ecosystems [*sensu* Higgs (2017)] that feature novelty we are only starting to understand (Lundholm and Walker, 2018), then more research is required to quantify the range of ecosystem services provided by the diversity and functional traits of plant species and assemblages. Although green roofs lack the complexity of many natural systems, their potential replicability could help to reveal key ecological process unique to the urban realm while providing valuable services at the same time (Felson and Pickett, 2005).

5. Conclusions

If EGRs are intended as green infrastructure solutions for an increasingly urbanising planet, then understanding the long-term performance of their vegetation and substrates is imperative. In spite of the shift in species and functional composition over time, the roofs surveyed supported multi-layered meadows, where Sedums formed a consistent ground cover beneath taller herbaceous species and small statured grasses. This recalls the German green roof industry’s original commitment to native ecosystems and plant communities (Krupka, 1985, Kolb and Schwarz, 1999), and suggests that the research and development behind that vision has been successful. Correspondingly, the same ecological design process should be extended to nascent green roof movements and industries, particularly bioregions where this technology is relatively new and where local or regional flora has yet to be explored. In addition to stress-tolerance, which can be expressed in various forms (not just succulent sedums), functional types involving ruderality and intermediary competitive forms are important components of resilient green roof vegetation. Having observed that mature green roof vegetation can feature a diversity of functional types, this study suggests that long-term floristic diversity may be facilitated by ensuring a diversity of traits and species from the start by providing spatial heterogeneity, and by considering the mechanisms that support persistence and those which determine colonisation.

List of Tables

Table 1. Original species lists for two extensive green roofs (with CSR signatures). The full dataset can be accessed at https://doi.org/10.15131/shef.data.5147146.v1 (see Thuring and Dunnett, 2017).

Both roofs	
Agrostis tenuis Sibth.	CSR
Dianthus deltoides L.	CSR
Digitaria sanguinalis L.	R
Festuca ovina L.	CSR
Hieracium pilosella L.	CSR
Inula hirta L.	SC
Linum perenne L.	SC
Nepeta racemosa Lam.	C
Onobrychis viciifolia Scop.	C
Plantago major L.	CSR
Poa compressa L.	CSR
Poa nemoralis L.	CSR
Polygonum aviculare L.	R
Potentilla argentea L.	CS
Rumex acetosella L. s. l.	CSR
Saponaria ocymoides L.	CS
Sedum acre L.	S
Setaria viridis (L.) P.B	R
Thymus pulegioides L.	CSR
Trifolium arvense L.	SR
Veronica spicata L.	SC
Killesberg only	
Potentilla crantzii auct. lusit.	CSR
Rathausgarage only	
Allium flavum L.	CSR
Dianthus carthusianorum L.	CSR
Saxifraga paniculata Mill.	CSR
Sedum album L.	S
Sedum kamtschaticum Fischer	S
Sedum hybridum L.	S
Sedum rupestre L.	S
Sedum sexangulare L.	S
Sedum spurium Bieb.	S
Sedum telephium L.	CS
Sempervivum tectorum L.	S
Silene uniflora Roth	CSR
Thymus serpyllum L.	CSR

Table 2. Persistence, loss and gain (%) for two Stuttgart roofs.

	Persistent	**Lost**	**Gained**
Killesberg	36.36	63.64	61.90
Rathaus	44.12	55.88	60.00
R-low	38.24	61.76	56.67
R-PV	44.12	55.88	42.31

Table 3. Percent cover (%) of functional types comprising the vegetation observed on two Stuttgart roofs.

Functional types present	**% cover**
S (stress tolerators)	50.92
CSR (CSR strategists)	28.06
R (ruderals)	7.79
SR (stress-tolerant ruderals)	7.29
C (competitors)	2.99
SC (stress-tolerant competitors)	2.92
CR (competitive ruderals)	0.04

Table 4. Occurrence (N) and relative frequency (RF) (total 47 plots) with mean cover for the top ten observed species. Species are arranged according to cover.

Species	**CSR**	**N**	**RF**	**Mean % cover**	**SE**		**Breakdown by strategies**
Sedum rupestre L.	S	45	0.96	55.30	5.31		CSR
Setaria viridis (L.) P.B	R	33	0.70	36.00	4.98		S
Crepis tectorum L.	CSR	29	0.62	21.89	3.39		R
Festuca ovina L.	CSR	22	0.47	19.60	4.89		SC
Sedum sexangulare L.	S	36	0.77	19.40	3.72		SR
Sedum hybridum L.	S	12	0.26	16.04	4.88		
Vulpia myuros L. C.C. Gmel.	SR	13	0.28	10.64	3.12		
Linum perenne L.	SC	27	0.57	10.38	2.17		
Dianthus carthusianorum L.	CSR	18	0.38	7.04	1.95		
Hieracium pilosella L.	CSR	11	0.23	6.32	2.75		

Table 5. Functional composition of mature green roof vegetation on two Stuttgart roofs for initial lists and observations in 2011, shown for each roof as a whole and for the distinct roof areas described.

Rathausgarage complex								
Initial (1990)		Observed (2011)	Rathaus (PV)	Wilcoxan Rank Test		Rathaus (lower)	Wilcoxan Rank Test	
SC/CSR		S/CSR	S/CSR	z-value	p	SR/CSR	z-value	p
C	0.305	0.138	0.123	3.464	0.001	0.151	3.352	0.001
S	0.462	0.57	0.597	2.947	0.003	0.539	2.953	0.003
R	0.233	0.292	0.28	3.464	0.001	0.31	3.35	0.001
Killesberg								
Initial (1991)		Observed (2011)	North-facing 2011	Wilcoxan Rank Test		South-facing 2011	Wilcoxan Rank Test	
CSR		S/CSR	S/CSR	z-value	p	S/SR	z-value	p
C	0.356	0.113	0.236	2.703	0.007	0.007	-2.862b	0.007
S	0.333	0.661	0.577	1.989	0.047	0.732	-1.886b	0.047
R	0.311	0.226	0.186	2.703	0.007	0.26	-2.701b	0.007

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