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Seasonal patterns of native plant cover and leaf trait variation on New York City green roofs

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Abstract
Plants make important contributions to green roof ecosystem service provision through evapotranspiration, canopy shading, and water retention. Because these plant communities are a critical component of green roof design and function, both seasonal and interspecific variation of these plant communities are important factors in evaluating green roof performance. This study examines variation in both species abundance and 9 leaf traits throughout the 2015 growing season of four New York City green roofs. While community composition varied significantly between each month ($p_{ANOSIM} = 0.036$), three major plant families (Asteraceae, Lamiaceae, and Poaceae) consistently had the greatest green cover and were present during the entirety of the growing season. For leaf traits, period of the growing season had a significant impact on most of the traits measured. Leaf thickness, leaf relative water content (RWC) and saturated water content (SWC) decreased as the growing season progressed, while leaf dry matter content (LDMC) and stomatal density increased, likely due to a seasonal decrease in rainfall as species-level variance in these water traits is low (7.40% and 0.88%, respectively). We also ranked planted and spontaneous species in accordance to both cover and functional trait values, and identified 11 species suitable for green roofs in NYC: *Pycnanthemum tenuifolium* (Lamiaceae), *Symphiotrichum leave, Symphiotrichum pilosum*, *Rudbeckia hirta*, *Solidago odora* (Asteraceae), *Panicum virgatum*, *Sorghastrum nutrans, Schizachyrium scoparium*, *Dichanthelium clandestinum*, *Deschampsia flexuosa* (Poaceae), and *Oenothera biennis* (Onagraceae). Understanding the temporal responses of plant communities and their constituent species is critical in optimizing green roof ecosystem services.

Keywords Biodiversity · Urban Ecology · Plant Traits · Native Plants · Green Infrastructure

Introduction

Green roofs are an increasingly popular alternative to traditional rooftops due to their aesthetic, hydrological, and thermal benefits, including mitigation of urban heat island effects, enhanced storm-water management, and reduced building energy costs (Monterusso et al. 2005; Oberndorfer et al. 2007; Villarreal 2007). These services heavily rely on the plant communities that live atop them and emphasize the need to plant species that can coexist in the harsh, drought-like conditions of the green roof environment while maintaining desired ecosystem services (Durhman et al. 2007; Blanusa 2013). A recent shift in green roof design from a single-genus (*Sedum*, sometimes called extensive green roofs) planting approach towards a high-diversity polyculture community (often called intensive or semi-intensive green roofs) has further highlighted a need to identify strong candidates to build these communities (Butler et al. 2012). In temperate cities like New York City (NYC), seasonal changes can have larger impacts on the timing of phenological events and presence of native plant species, unlike their evergreen *Sedum* counterparts. This results in temporal variation in native plant functional traits and therefore green roof function during the growing season, even if annual ecosystem function remains similar. Because of this, both native plant species identity and behavior is critical in maintaining and optimizing green roof ecosystem function as the

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seasons progress (MacIvor and Lundholm 2011; Durhman et al. 2007).

Seasonal variation of green roof performance has been a difficult quality to assess as much of the literature focuses on either whole-roof ecosystem function and construction or plant species identity and survival, rather than plant community dynamics over a growing season. Plant community composition, for example, is a key component of green roof function, as the seasonal rise and fall of species can have profound effects on rates of stormwater retention, evapotranspiration, shading, and therefore cooling (Getter et al. 2009; Blanusa et al. 2013). Some broader plant community metrics have also shown enhanced performance, such as increasing plant species richness reducing green roof nutrient run-off (Johnson et al. 2016). Plant species identity can further exacerbate this, as interspecific variation in phenology can result in large swings of peak activity and therefore green roof ecosystem functions, especially on intensive green roofs (Nagase et al. 2013; Peng and Jim 2015). Because green roof function is intimately tied to the living plants atop them, a failure to recognize fluctuations in plant community composition is a failure to meet financial and ecosystem service needs of the stakeholders.

Quantifying the seasonal functional changes in green roof plant community composition is complex, however, a morphological leaf trait-based approach to native plant species selection and plant community assemblage is an effective method in assessing ecosystem function (Lundholm et al. 2015; Balachowski and Volaire 2018). Leaf traits such as relative water capacity (RWC) and leaf dry matter content (LDMC) can be used to infer some of the ecophysiological parameters related to ecosystem function like stormwater retention (Villarreal et al. 2007). These traits are also plastic with respect to environmental conditions at the time of leaf formation, but are relatively inelastic after leaf maturity and highlights interspecific differences in growth and survival of these plants. For example, leaf mass per area (LMA) and leaf thickness (L_{th}) can be used to infer primary productivity and water loss, both of which may be important green roof functions, but also indicate more succulent leaves that can withstand the higher temperatures and light intensity (Durhman et al. 2007). By using a suite of leaf traits that account for several green roof functions and plant survival strategies, native plant species can be ranked and summarized seasonally based on their leaf traits to inform better inform stakeholders and building managers.

In this study, we examine green roof plant community composition and trait variation to inform planting decisions of native species for green roofs. We report on variation of plant community composition of green roofs 4–5 years after initial planting on public buildings in NYC, a temperate city. Specifically, we examine seasonal variability in species presence, absence, and morphological leaf traits, which together influence ecosystem function (Garnier and Navas 2011; Van Mechelen et al. 2014). We use our data to rank these plant species according to both potential for green roof ecosystem function and abundance. We hypothesize that 1) native plant species that have high rankings in drought-tolerance traits will have the greatest abundance, and 2) the leaf traits related to drought tolerance will increase, as water availability decreases in the late season.

Methods

Study sites

Four green roofs throughout NYC were assessed monthly from May through October 2015. These four roofs were located atop three NYC Parks Department Recreation Centers (Jackie Robinson, Hansborough, and St. Mary's) and one atop Barnard College's Diana Center. All four green roofs are within 800 ha of each other (40 N, 73 W), approximately 50 m above sea level, and experience similar weather and climate. The three recreation center roofs were retrofitted with green roofs using identical designs and source materials in 2010, while the Diana Center green roof was installed on a newly constructed building and planted with a substantially overlapping selection of plant species in 2011 (for further details, see McGuire et al. 2013 and Aloisio et al. 2017). Sites were

Table 1 Leaf traits measured on four New York City green roofs. Ecosystem services of green roofs are dependent on biological processes, which can be inferred from numerous leaf characteristics

Trait	Units	Inference
Leaf Mass per Area (LMA)	mg/mm^2	Leaf longevity, shape, light competition
Leaf Dry Matter Content (LDMC)	mg/g	Leaf longevity, construction, photosynthesis
Leaf Thickness (L_{th})	mm	Leaf longevity, construction, water storage
Relative Water Content (RWC)	%	Water balance
Saturated Water Content (SWC)	g/mm^2	Water balance
Stomatal Density	$Stomates/mm^2$	Water balance, gas exchange
C:N	-	Plant nutrition, carbon storage
δ13C	‰	Water balance, photosynthesis
δ15N	‰	Plant nutrition

visited from May to October 2015, identified to the species level, and leaves were collected for a suite of leaf trait measurements (See Table 1).

NYC Parks Recreation Center green roofs were established with 12 plots measuring 2 m x 4 m, subdivided into two 2 m x 2 m subplots via a thin wooden beam. Subplots used in this study had an initial media depth of 15 cm and composed of 6.8% silt, 36.2% sand, and 57% gravel, with a pH of 7.8 and organic matter content of 4% (Aloisio et al. 2017). A total of 6 subplots were planted with Hempstead Plains communities, and 6 subplots of Rocky Summit communities. For the purpose of this study, all analyses treat the entire green roof as a single community due to substantial degrees of overlap since construction. Recreation center green roofs have not been irrigated since initial planting in 2010. Roof exposure to sunlight varied across some of the roofs due to differences in height of neighboring buildings (Aloisio et al. 2017).

All roofs shared 16 planted species drawn from the species pool of grasslands in the region, with eight selected to mimic New York State's Hempstead Plains community and 8 mimicking Rocky Summit habitats (Tables 2 and 3; Edinger et al. 2014). The Hempstead Plains is a critically endangered habitat in NY state, originally encompassing more than 16,000 ha and now reduced to a roughly 8 ha preserve due to changes in land use and habitat degradation (Neidich-Ryder and Kennelly 2014). The Rocky Summit grassland community occurs throughout Lower New England and the Hudson Highlands in NY state (McGuire et al. 2013). Plants were initially grown from seed at the NYC Green Belt Native Plant Center (Staten Island, NY) before planting until an initial green cover of 12.5% (Aloisio et al. 2017). Only plots initially planted with the same set of 16 species native to the Hempstead Plains and Rocky Summit habitats were used in this study, along with any spontaneously recruited species that established within those plots (Tables 2 and 3).

The Diana Center Green roof at Barnard College differs from the other roofs, as it is embedded into the roof infrastructure, rather than retrofitted atop a traditional roof. In addition, this roof is accessible to certain Barnard College staff members and is used for organizing Barnard College events, as well as undergraduate science courses. Eight plots are configured in a long, trapezoidal shape with two plots ("Pollinator" and "Sedum") planted with a different suite of plant species (Fig. 1). These plots are adjacent to an area of turfgrass. Of the eight plots, only three were used in this study: RS Random ($9m^2$), RS Plotted ($8m^2$), and HP Random ($7m^2$), where "Random" plots had initial plantings in a random patterm, while "Plotted" plots were planted in a uniform grid design. Media depth was approximately 20 cm in each plot. There was unintended and sporadic irrigation of the entire roof in May and early June 2015 due to unseasonably dry conditions.

Green cover estimates and tissue collection

Each plot was subdivided into eight sections and four of these sections were selected for observation from May–October 2015 (two RS and two HP each). A $0.25m^2$ quadrat with 5 cm markings on each side was laid on each section, and percent cover was estimated for each species present in the quadrat and relativized across the roof. Only individuals taller than 5 cm in height or extending at lease 5 cm along the ground were considered for leaf collection. Individuals consisting of only juvenile basal rosettes or dried leaves were excluded. Specifically, we adjusted green cover here in order to compare green roof across parts of the growing season, as the early and late parts of the growing season can have very low absolute green cover (hereon relative green cover).

After measuring cover, three to six fully-expanded leaves, regardless of number of leaflets, were collected from each species in each plot, and placed into a sealed plastic bag with a moistened paper towel for leaf trait analysis. Healthy, fully-expanded, non-basal leaves were collected from different individuals where possible. Leaves were processed in the laboratory within 12 h of collection.

Leaf traits—leaf morphology and water content

All leaves were measured via the protocols described in (Cornelissen 2003). Three leaves were immediately scanned in a flatbed scanner for leaf area measurements using ImageJ (Schneider et al. 2012). Leaves were then weighed in a standard balance for fresh weight to the nearest mg and L_{th} was measured using digital calipers. For compound leaves, L_{th} was measured for all leaflets, which were then averaged per whole leaf. Following these measurements, leaves were then floated in R_o water in 20 mL scintillation vials in a moderately lit cold room for 18–24 h. Leaves were removed from cold storage, gently dried, and reweighed for saturated leaf mass. Finally, leaves were placed into labeled coin envelopes and dried in an incubator for at least three days at 60^o C. All petioles and rachises were left intact and included as part of the leaf measurements. Traits were calculated as follows (Cornelissen et al. 2003):

$$LMA = Md/A \tag{1}$$

$$LDMC = Md/Mt \tag{2}$$

$$RWC = 100(Mf - Md)/(Mt - Md) \tag{3}$$

$$SWC = Mt/A \tag{4}$$

Table 2 Species found on NYC Green Roofs and corresponding trait values. All species represented on the four green roofs located at the Diana Center (Barnard College), Jackie Robinson Park Recreation Center, St. Mary's Park Recreation Center, and Hansborough Recreation Center. Recruited species arrived independently into plots after original plantings of Hempstead Plains and Rocky Summit species. Plant community types (CT) include Hempstead Plains (HP), Rocky Summit (RS), and Recruited plant communities. Plant traits shown below represent overall mean values ± 1 standard deviation, and include Leaf Thickness (L_{th}), Leaf Mass per Area (LMA), Leaf Dry Matter Content (LDMC), Relative Leaf Water Content (RWC), Saturated Leaf Water Content (SWC), and Stomatal Density (SD)

Species	CT	L_{th} (mm)	LMA (mg/mm^2)	LDMC (mg/g)	RWC (%)	SWC ($g/mm^2 \times 10^{-4}$)	SD (per mm^2)
Asclepias tuberosa	HP	0.13 ± 0.02	0.058 + 0.024	224.93 ± 24.24	61.90 ± 7.17	2.58 ± 0.69	354.12 ± 80.46
Baptisia tinctoria	HP	0.15 ± 0.01	0.051 ± 0.005	244.15 ± 25.78	79.76 ± 8.45	2.12 ± 0.23	225.07 ± 89.55
Eupatorium hyssopifolium	HP	0.22 ± 0.02	0.062 ± 0.008	190.82 ± 19.40	71.29 ± 5.13	3.29 ± 0.40	104.00 ± 26.27
Panicum virgatum	HP	0.012 ± 0.03	0.076 ± 0.029	325.10 ± 34.16	70.64 ± 12.57	2.37 ± 0.91	181.83 ± 49.64
Schizachyrium scoparium	HP	0.09 ± 0.01	0.048 ± 0.009	308.40 ± 40.40	50.52 ± 13.26	1.58 ± 0.24	255.67 ± 47.35
Solidago nemoralis	HP	0.19 ± 0.02	0.066 ± 0.017	253.14 + 36.51	83.20 ± 4.75	2.68 ± 0.61	226.67 ± 69.1
Sorghastrum nutans	HP	0.11 ± 0.03	0.060 ± 0.22	301.54 ± 37.37	57.33 ± 18.18	2.00 ± 0.65	204.55 ± 51.48
Symphyotrich laeve	HP	0.21 ± 0.05	0.079 ± 0.032	220.75 ± 29.31	61.47 ± 10.69	3.55 ± 1.31	222.81 ± 42.21
Danthonia spicata	RS	NA	NA	NA	NA	NA	NA
Deschampsia flexuosa	RS	0.14 ± 0.03	0.085 ± 0.041	327.84 ± 65.56	55.90 ± 21.55	2.55 ± 1.16	243.54 ± 87.44
Dichanthelium clandenstinum	RS	0.13 ± 0.03	0.042 ± 0.013	222.79 ± 30.03	57.84 ± 12.91	1.93 ± 0.54	130.79 ± 25.01
Ionactis linariifolius	RS	NA	NA	NA	NA	NA	NA
Lespedeza capitata	RS	0.14 ± 0.02	0.072 ± 0.013	346.23 ± 25.96	62.83 ± 14.57	2.07 ± 0.30	382.10 ± 79.11
Pycnanthemum tenuifolium	RS	0.16 ± 0.03	0.063 ± 0.026	261.24 ± 109.56	62.21 ± 21.64	2.42 ± 0.37	207.06 ± 47.64
Rudbeckia hirta	RS	0.25 ± 0.04	0.054 ± 0.006	152.05 ± 14.91	57.74 ± 9.90	3.61 ± 0.40	219.56 ± 51.16
Solidago odora	RS	0.13 ± 0.02	0.051 ± 0.007	276.70 ± 30.34	71.61 ± 6.73	1.89 ± 0.21	295.63 ± 92.93
Acer spp.	R	NA	NA	NA	NA	NA	NA
Ambrosia artemisiifolia	R	NA	NA	NA	NA	NA	NA
Artemisia vulgaris	R	0.14 ± 0.01	0.063 ± 0.016	219.01 ± 4.38	56.00 ± 4.27	2.91 ± 0.76	NA
Cerastium vulgatum	R	NA	NA	NA	NA	NA	NA
Chenopodium album	R	NA	NA	NA	NA	NA	NA
Digitaria ciliaris	R	0.06 ± 0.01	0.034 ± 0.002	213.83 ± 27.51	32.79 ± 6.14	1.68 ± 0.13	117.33 ± 31.23
Echinochloa crus-galli	R	0.10 ± 0.01	0.063 ± 0.005	263.25 ± 13.57	47.29 ± 7.22	2.37 ± 0.09	29.33 ± 18.70
Euphorbia maculata	R	0.09 ± 0.01	0.028 ± 0.002	165.28 ± 20.85	70.79 ± 19.21	1.75 ± 0.11	90.67 ± 26.13
Galium aparine	R	NA	NA	NA	NA	NA	NA
Oxalis stricta	R	0.11 ± 0.01	0.027 ± 0.008	178.42 ± 41.85	83.29 ± 9.01	1.56 ± 0.26	NA
Oenothera biennis	R	0.22 ± 0.04	0.064 ± 0.015	151.45 ± 17.91	69.99 ± 6.40	4.28 ± 1.04	186.67 ± 46.19
Parthenocissus quinquefolia	R	NA	NA	NA	NA	NA	NA
Poa annua	R	NA	NA	NA	NA	NA	NA
Poa pratensis	R	NA	NA	NA	NA	NA	NA
Poa spp.	R	NA	NA	NA	NA	NA	NA
Portulaca oleracea	R	NA	NA	NA	NA	NA	NA
Pycnanthemum virginianum	R	0.12 ± 0.01	0.043 ± 0.004	184.06 ± 10.11	41.11 ± 5.11	2.27 ± 0.10	186.67 ± 33.31
Quercus spp.	R	NA	NA	NA	NA	NA	NA
Setaria faberi	R	0.09 ± 0.03	0.036 ± 0.019	225.01 ± 48.62	51.55 ± 16.95	1.61 ± 0.73	183.68 ± 50.48
Stellaria media	R	0.15 ± 0.01	0.040 ± 0.008	154.76 ± 29.96	45.30 ± 8.87	2.54 ± 0.05	NA
Symphyotrichum novae-angliae	R	0.13 ± 0.03	0.046 ± 0.009	169.64 ± 22.30	42.48 ± 11.46	2.74 ± 0.56	389.93 ± 93.32
Symphyotrichum pilosum	R	0.15 ± 0.04	0.058 ± 0.014	216.20 ± 38.68	58.91 ± 15.73	2.68 ± 0.50	184.18 ± 57.53
Taraxacum officinale	R	NA	NA	NA	NA	NA	NA
Trifolium campestre	R	0.12 ± 0.01	0.060 ± 0.021	254.90 ± 29.89	81.22 ± 3.57	2.31 ± 0.64	351.11 ± 64.00
Ulmus americana	R	NA	NA	NA	NA	NA	NA
Vicia sativa	R	NA	NA	NA	NA	NA	NA
Unidentified Weed	R	NA	NA	NA	NA	NA	NA

Table 3 Species found on NYC Green Roofs and corresponding trait values. All species represented on the four green roofs located at the Diana Center (Barnard College), Jackie Robinson Park Recreation Center, St. Mary's Park Recreation Center, and Hansborough Recreation Center. Recruited species arrived independently into plots after original plantings of Hempstead Plains and Rocky Summit species. Plant community types (CT) include Hempstead Plains (HP), Rocky Summit (RS), and Recruited plant communities. Plant traits shown below represent overall mean values ± 1 standard deviation, and include the isotopic ratios of C-12 and C-13 (δ13C) and N-14 and N-15 (δ15N), and C:N ratio

Species	CT	δ13C (‰)	δ15N (‰)	C:N
Asclepias tuberosa	HP	-29.260 + 0.992	1.960 ± 1.860	18.723 ± 2.408
Baptisia tinctoria	HP	-30.549 + 0.357	-0.479 ± 0.070	16.394 ± 2.283
Eupatorium hyssopifolium	HP	-31.400 + 0.102	-0.458 ± 0.204	28.949 ± 0.866
Panicum virgatum	HP	-14.158 + 0.334	0.739 ± 1.508	25.205 ± 2.012
Schizachyrium scoparium	HP	-13.536 ± 0.336	3.057 ± 4.425	39.145 ± 4.266
Solidago nemoralis	HP	-30.899 ± 0.812	3.603 ± 3.058	21.395 ± 2.079
Sorghastrum nutans	HP	-14.856 ± 0.120	3.413 ± 1.144	34.701 ± 2.698
Symphyotrichum leave	HP	-30.209 ± 0.538	2.807 ± 0.997	25.947 ± 1.986
Danthonia spicata	RS	NA	NA	NA
Deschampsia flexuosa	RS	-28.411 ± 0.162	4.981 ± 0.738	46.370 ± 3.417
Dichanthelium clandenstinum	RS	-29.192 ± 0.286	1.787 ± 1.022	26.005 ± 1.908
Ionactis linariifolius	RS	NA	NA	NA
Lespedeza capitate	RS	-28.901 ± 0.341	-1.943 ± 0.115	23.663 ± 1.087
Pycnanthemum tenuifolium	RS	-30.660 ± 0.346	2.540 ± 2.016	28.963 ± 4.464
Rudbeckia hirta	RS	-30.618 ± 1.433	3.893 ± 3.821	23.177 ± 2.256
Solidago odora	RS	-32.453 ± 0.948	-0.298 ± 0.330	35.384 ± 1.787
Acer spp.	R	NA	NA	NA
Ambrosia artemisiifolia	R	NA	NA	NA
Artemisia vulgaris	R	-31.280 ± 0.057	-0.275 ± 0.035	16.335 ± 0.201
Cerastium vulgatum	R	NA	NA	NA
Chenopodium album	R	NA	NA	NA
Digitaria ciliaris	R	-13.315 ± 0.035	6.430 ± 0.184	25.177 ± 0.160
Echinochloa crus-galli	R	NA	NA	NA
Euphorbia maculate	R	NA	NA	NA
Galium aparine	R	NA	NA	NA
Oxalis stricta	R	-30.804 ± 0.047	4.608 ± 0.233	24.992 ± 2.070
Oenothera biennis	R	-27.653 ± 0.321	1.038 ± 0.115	18.111 ± 0.214
Parthenocissus quinquefolia	R	NA	NA	NA
Poa annua	R	NA	NA	NA
Poa pratensis	R	NA	NA	NA
Poa spp.	R	NA	NA	NA
Portulaca oleracea	R	NA	NA	NA
Pycnanthemum virginianum	R	-29.300 ± 0.028	7.668 ± 0.117	23.564 ± 0.169
Quercus spp.	R	NA	NA	NA
Setaria faberi	R	-13.811 ± 0.114	7.499 ± 0.476	19.751 ± 1.500
Stellaria media	R	NA	NA	NA
Symphyotrichum novae-angliae	R	-31.119 ± 0.599	0.823 ± 0.398	22.945 ± 1.881
Symphyotrichum pilosum	R	-31.502 ± 0.198	1.998 ± 1.237	23.400 ± 1.732
Taraxacum officinale	R	NA	NA	NA
Trifolium campestre	R	-29.750 ± 0.187	-1.450 ± 0.061	14.738 ± 0.633
Ulmus Americana	R	NA	NA	NA
Vicia sativa	R	NA	NA	NA
Unidentified Weed	R	NA	NA	NA

where M_f, M_d, and M_t are fresh, dry, and turgid mass, respectively, and A is leaf area. High values of LMA are generally reflective of high leaf investment and longer leaf lifespans, and is the inverse of specific leaf area (SLA; not presented). LDMC relates to leaf tissue density, and scales positively with LMA. RWC is the percentage of leaf mass contributed by water as measured soon after collection (*i.e.*, an instantaneous measure of leaf water content), whereas SWC, though less commonly used, is the absolute, maximum mass of water within the leaf per mm.

Leaf traits—stomatal density

Stomatal density was measured using three leaves different from the ones used for the other leaf trait measurements. The underside of each leaf was painted with a clear nail polish

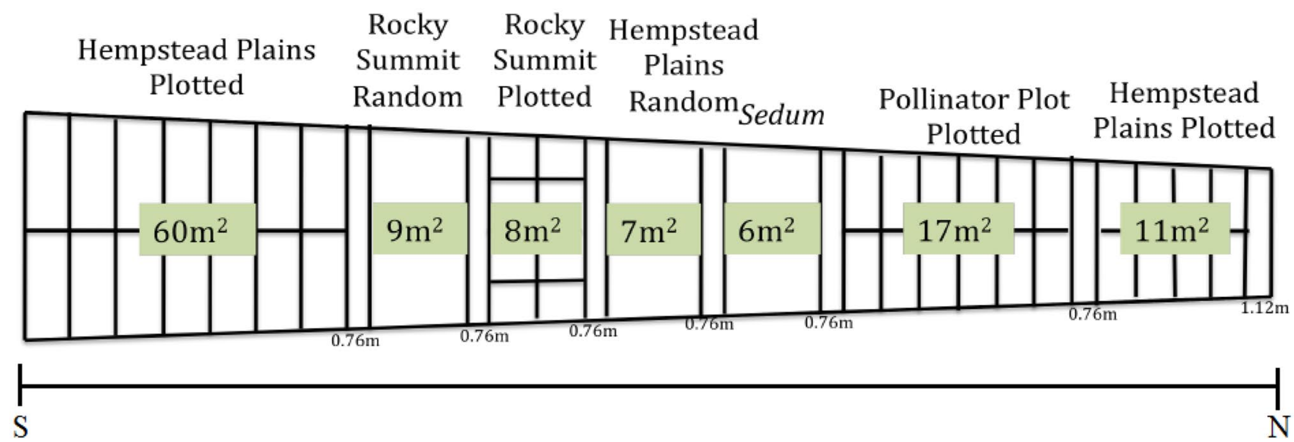

Fig. 1 Layout of the Barnard College Diana Center Roof. Plots with random species plantings were labeled as "random", whereas organized, structured plots were labeled "plotted". Plots used in this study were Rocky Summit Random ($9m^2$), Rocky Summit Plotted ($8m^2$), and Hempstead Plains Random ($7m^2$) (adapted from Hyson 2012)

(*Wet n' Wild: Wild Shine*™ *Clear Nail Protector*, Markwin's Beauty Products, Inc., China) and allowed to dry for approximately 15 min. Clear tape was then pressed to the painted side of the leaf and carefully peeled off, before being transferred to a microscope slide. Slides were then viewed in a compound microscope at 400X magnification, and stomates were counted within a $0.0625mm^2$ reticle so long as > 50% of the stomate was within the reticle. Stomatal counts were then multiplied by 16 to calculate stomatal density per mm^2.

Leaf traits—isotopic composition

Following fresh, turgid, and dry leaf measurements, leaves from each species were pooled across plots from each roof in order to obtain sufficient mass for isotopic analysis ($n_{total}=163$). Leaf samples were measured using an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA) and analyzed via continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen) at the Washington State University Stable Isotope Core laboratory.

Table 4 Period of the growing season has a significant effect on all measured leaf traits except isotope traits δ13C and δ15N. The effects of period during the growing season in a linear mixed effects model (Eq. 5) on all measured leaf traits of green roof plants, where species and location are random effects

Trait	χ^2	*df*	*p-value*
L_{th}	16.518	2	0.0003***
LMA	10.941	2	0.0042**
LDMC	14.297	2	0.0008***
RWC	63.538	2	1.596×10^{-14}***
SWC	15.214	2	0.0005***
Stomatal Density	26.916	2	0.0424*
δ13C	2.458	2	0.2926
δ15N	4.235	2	0.1203
% C	28.66	2	5.978×10^{-7}***
% N	10.04	2	0.006605**
C:N	63.197	2	3.73×10^{-5}***

Species rankings

Species were ranked based on each measured leaf trait and relative green cover, and separated by period of the growing season. Growing season period was categorized into "Early", "Int", and "Late" seasons for leaf trait analysis, with each category composed of two months of the growing season (May and June, July and August, and September and October, respectively). Highly ranked species (i.e. Ranks 1–10) had high values in the measured trait/cover as these are the traits that are highly desired of green roof plants in NYC, with the exception of stomatal density (where low stomatal density counts were considered higher rank, suggesting greater water retention). The mean trait rank was produced by ranking each of the trait values for each species, then taking the mean of these trait ranks.

Statistical analysis

All statistical analyses and data graphics were done using R (R Core Team 2019) and figures were produced using *ggplot2* (Wickham 2016), *ggbiplot* (Vu 2011), and *cowplot* (Wilke 2019). Only species which occurred more than two times in the growing season were included in the analyses of similarity (ANOSIM) to assess temporal variation of species across green roofs using dissimilarity matrices. Raup-Crick criterion were applied to the data using metanonmetric multidimensional scaling (metaMDS) with one million repetitions (Anderson et al. 2011). ANOSIM and metaMDS were both performed using the *vegan* package (Oksanen et al. 2019).

Table 5 Some leaf traits vary more with respect to species identity, while vary more with environment. Variance of the random effects of the linear mixed-effects model (Eq. 5), with the proportion of random effect variance in parentheses. LDMC and molecular traits attribute the majority of their variance to species identity, while RWC attributes more to residual effects

Trait	*Spp*		*Location*		*Residual*	
L_{th}*	2.42×10^{-3}	(77.50)	8.33×10^{-5}	(2.67)	6.21×10^{-4}	(19.88)
LMA*	1.69×10^{-4}	(35.10)	1.45×10^{-5}	(3.01)	2.98×10^{-4}	(61.89)
LDMC	2583.18	(51.66)	1.27	(0.03)	2415.97	(48.32)
RWC	19.02	(7.40)	60.87	(23.69)	177.03	(68.90)
SWC*	2.99×10^{-9}	(0.88)	3.33×10^{-7}	(98.20)	3.12×10^{-9}	(0.92)
Stomatal Density	6692.0	(66.46)	266.2	(2.64)	3111.4	(30.90)
δ13C	45.824	(97.46)	NA	NA	1.196	(2.54)
δ15N	4.347	(50.45)	NA	NA	4.270	(49.55)
% C	3.391	(64.30)	NA	NA	1.883	(35.70)
% N	0.1729	(49.58)	NA	NA	0.1758	(50.42)
C:N	44.68	(61.55)	NA	NA	27.91	(38.45)

*L_{th}, LMA, and SWC variance are roughly 3 orders of magnitude smaller than mean measurements, and thus are negligible

Linear mixed-effects models were used to understand variation in each trait across the growing season and compared to a null model with the Wald test using the R package *lme4* (Bates et al. 2015). The models are as follows:

$$LME.Trait = lme(Trait \sim Growing.Season + (1|Species) + (1|Location) \quad (5)$$

$$LME.TraitNull = lme(Trait \sim 1 + (1|Species) + (1|Location) \quad (6)$$

where Trait represents the mean of each trait value per species and Growing.Season is a fixed effect composed of the three periods of the growing season (Early, Intermediate, Late). Species is encoded as a random effect to account for variation in natural species recruitment, while Location is considered random due to inherent variations in roof dynamics (i.e. degree of sun and wind exposure).

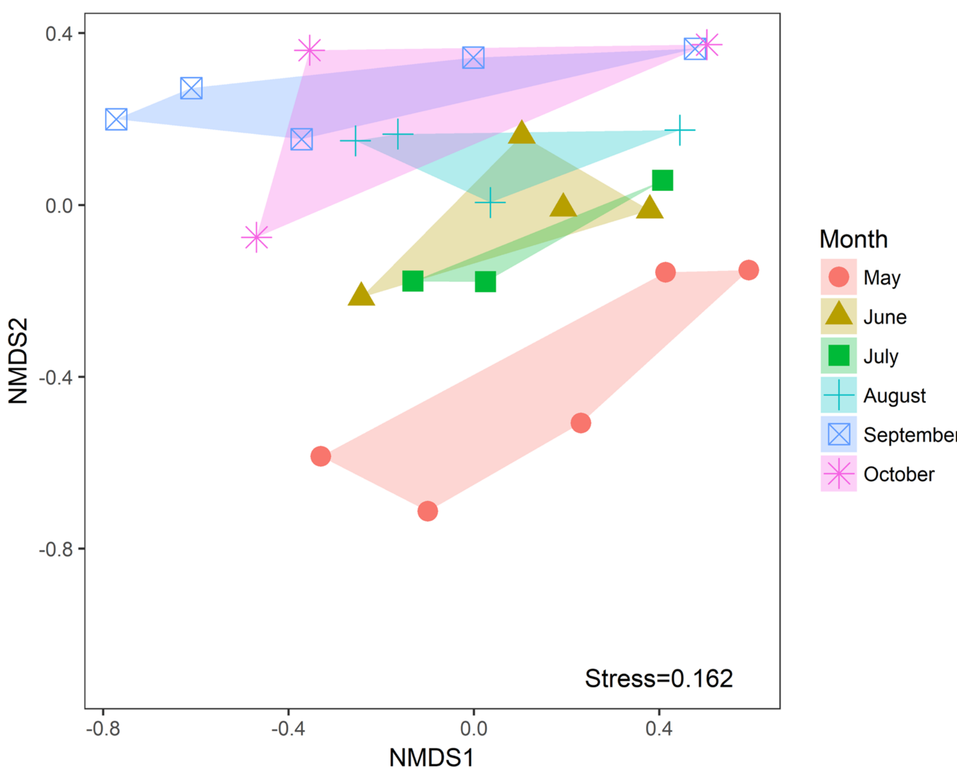

Fig. 2 Plant species on green roofs occur during different times of the growing season. Each point of this multi-dimensional space represents a sampling event ($n=24$). Polygons represent the breadth of species presence and absence during each month of the growing season, and limited overlap indicates that the composition of plant communities varies between months of the growing season ($R_{ANOSIM}=0.172$, p = 0.036, MetaMDS Stress = 0.162)

Results

Species presence-absence

In total, 42 species were observed in this study, and nine traits were measured (Table 2). Leaf trait information was measurable from 26 species. *Danthonia spicata* and *Ionactis linariifolius* were the only two species of the 16 planted initially on all four roofs that were extirpated across all four green roofs. The other 14 initially planted species were present on all four roofs sampled in this study.

Species occurrences vary temporally over the course of the growing season ($R_{ANOSIM} = 0.172$, $p_{ANOSIM} = 0.046$; $Stress_{MetaMDS} = 0.162$; Fig. 2). Importantly, polygons representing months of the growing season exhibit some degree of overlap, but are separated and the ordination overall has relatively low stress (Fig. 2). Throughout the growing season, patterns of abundance shifted with the most abundant species in the early season changing in both intermediate and late seasons (Fig. 3). Eight species present at all times: *Symphyotrichum laeve, Symphyotrichum pilosum* (Asteraceae), *Pycnanthemum tenuifolium* (Lamiaceae), *Dichanthelium clandestinum, Panicum virgatum, Sorghastrum nutans, Deschampsia flexuosa,* and *Setaria faberi* (Poaceae). Notably, *Pycnanthemum tenuifolium*, *Panicum virgatum*, and *Setaria faberi* had consistently high relative green cover throughout the season. In all cases, all initially planted species have deviated from their original coverages since their planting in 2010 and 2011 (i.e. greater or less than 12.5%).

Trait & isotope analyses

Linear regressions comparing LMA, LDMC, L_{th}, RWC, and SWC are aggregated across all sites and sampling events (Fig. S1). Traits increase linearly with each other, and that these correlations are significant ($p < 0.05$) though weak. We examined in further detail the L_{th}, LMA, LDMC, and RWC in the top five most abundant (i.e. highest relative green cover) species (*Pycnanthemum tenuifolium*, *Poa virgatum*, *Sateria faberi*, *Sorghastrum nutans*, and *Schizachyrium scoparium*), as these measures are commonly used leaf traits in plant ecophysiological studies and may indicate the strategies that these species have adopted (Fig. 4). Notably, RWC decreases for all five species as the season progresses as expected.

Growing season period affects all measured traits ($p < 0.05$; Table 4) with the exception of δ13C and δ15N isotopic composition. For some traits, other factors in the

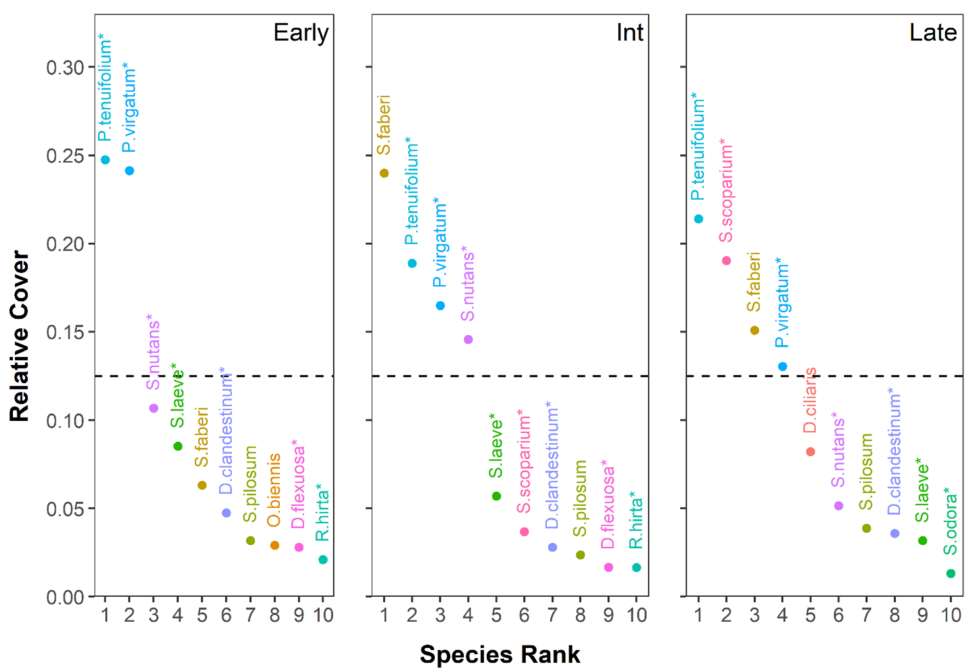

Fig. 3 Green roof species cover and dominance changes depending on the time of the growing season. Relative green cover is used due to low green cover in the earliest and latest parts of the growing season, and estimates whole-roof cover. Colors are for visual effect only, and the dashed line indicates the initial cover of the planted species (12.5%). At the time of this study, nearly all of the plant species have deviated from the original green cover percentage. Eight species (*Symphiotrichum laeve, Symphiotrichum pilosum, Pycnanthemum tenuifolium, Dichanthelium clandestinum, Sorghastrum nutans, Deschampsia flexuosa,* and *Setaria faberi*) are dominant during all times of the growing season, while two species (*Schizachyrium scoparium* and *Digitaria ciliaris*) also rapidly increase in cover in the intermediate and late growing seasons, respectively. Asterisks indicate initially planted species, while all others were recruited naturally since initial construction of the green roofs

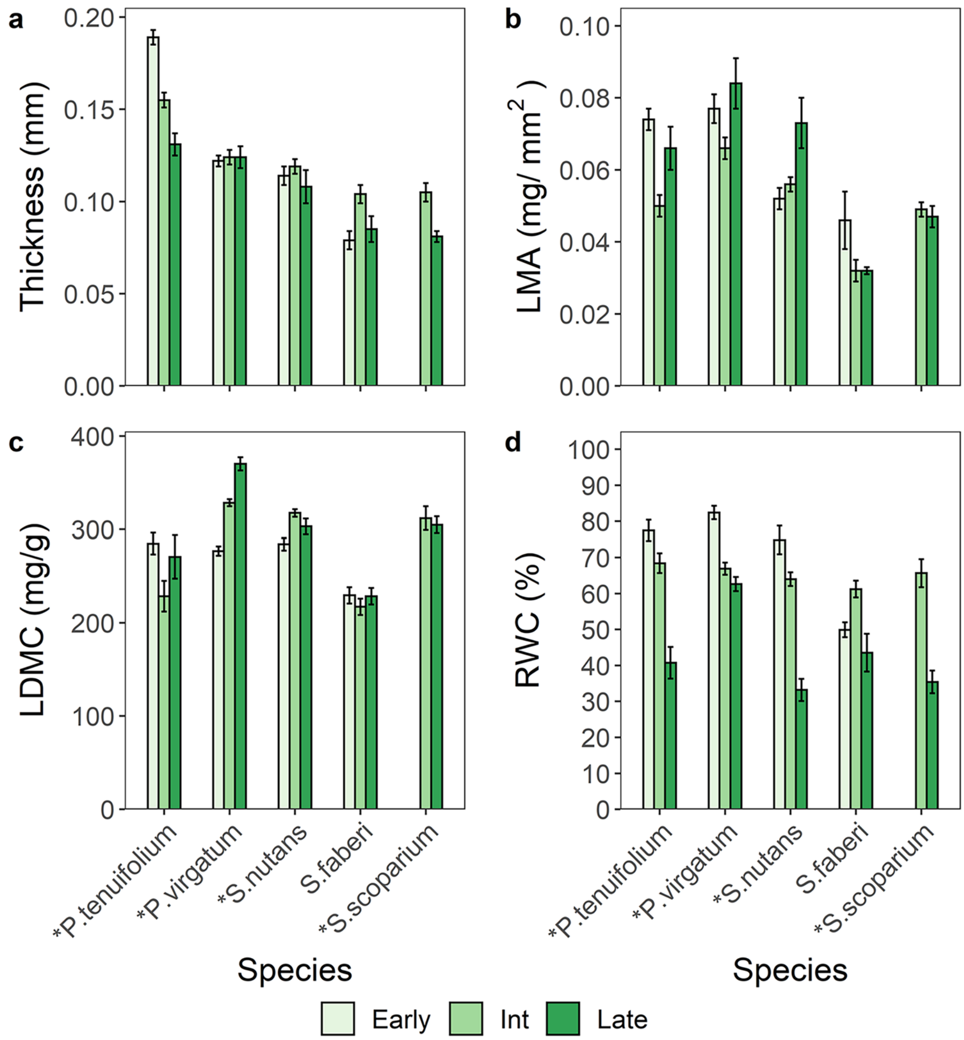

Fig. 4 **a-d** Subset of average trait measurements of the three highest abundance plant species on NYC green roofs in each of the three parts of the growing season (Early, Int, Late). LDMC increases as the growing season progresses for most of the species, likely due to increasing temperatures and sunlight, with decreasing rainfall frequency. Both leaf thickness and LMA seem to exhibit species-dependent drought resistance strategies. RWC decreases in most species, however, it is the most sensitive leaf trait measured in this study to available water at the time of collection. Of the 24 field visitations, leaves were only available for collection on 18 field visits

study design were also important sources of variation for several other traits. The model explains L_{th}, LMA, and SWC well, as the variance of random effects is smaller than the mean measure of each trait by three orders of magnitude, and is thus negligible (Table 5). We also observed a close relationship between LDMC, stomatal density, and leaf composition traits (δ13C, δ15N, %C, %N, and C:N) with species identity, all of which attribute roughly 50% or more of their total variance to species identity (Table 5). Conversely, SWC variance is strongly attributed to location of the green roof (98.20%). Finally, the variance of LMA and RWC are attributed to predominantly residual effects (> 50%).

Species rankings

Species were ranked from highest (i.e. Rank 1) to lowest (i.e. Rank 26) for relative green cover and all measured traits across the growing season. We focus here on the top 10 highest ranking species in relative green cover and mean trait ranking (Figs. 3 and 5). While the most abundant species in each season tended to rank very highly in regards to leaf traits (i.e. *Pycnanthemum tenuifolium* and *Panicum virgatum*), some less abundant species also ranked highly in leaf traits. Of particular note is *Setaria faberi*, a noxious weed and invasive species in much of North America (USDA, NRCS 2019), which ranked very highly in relative green cover (5th in Early, 1st in Int, and 3rd in Late), but poorly in leaf traits (lower than 10th place in all parts of the growing season). In addition, *Symphiotrichum pilosum* and *Oenothera biennis* were the only spontaneous species (i.e. not part of the initial planting) to place in the top 10 ranking for both relative green cover and leaf traits (Fig. 5).

Discussion

In this study, we find that highly abundant species on these green roofs included *Pycnanthemum tenuifolium* (Lamiaceae), *Panicum virgatum,* and *Sorghastrum nutans*

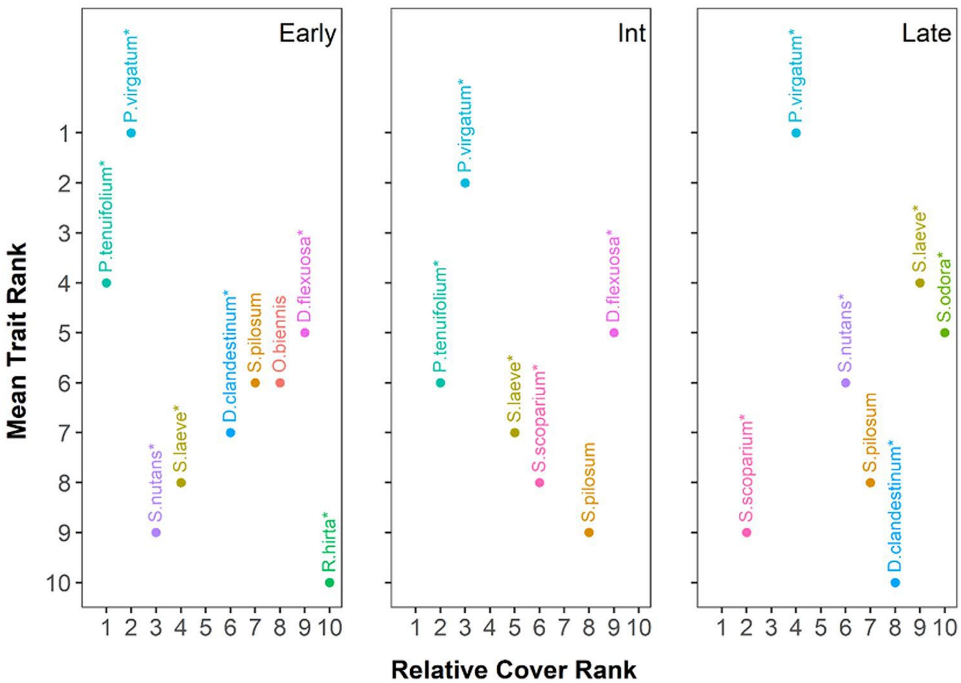

Fig. 5 Green roof plant species that may not be the most abundant are not necessarily poor green roof species, and can rank higher in relevant leaf traits than more abundant plant species. Each leaf trait measured was ranked for each species, averaged, then re-ranked. Relative green cover is used due to low green cover in the earliest and latest parts of the growing season, and estimates whole-roof cover. Colors are for visual effect only. Species that were ranked very highly in cover, but very poorly in leaf traits are *Setaria faberi* (all seasons), *Dichanthelium clandestinum* (Int), *Rudbeckia hirta* (Int), *Pycnanthemum tenuifolium* (Late), and *Digitaria ciliaris* (Late), which have fallen outside of the bounds of this figure of top 10 ranks. This indicates that these species may not be contributing to green roof function as strongly, despite their high abundance, at these times in the growing season. Of particulate note is *S. faberi*, which is highly abundant throughout the growing season, but ranks poorly in leaf traits

(Poaceae), and is consistent with our first hypothesis that native plant species ranking highly in drought-tolerance leaf traits will be highly abundant (Fig. 5). However, *Setaria faberi* (Poaceae) also had exceptionally high abundance despite ranking poorly in leaf traits. Secondly, we find that leaf traits varies significantly with the period of the growing season, however, the trends they exhibit appear to be species specific. Other notably abundant species include *Symphiotrichum laeve*, *Symphiotrichum pilosum*, and *Dichanthelium clandestinum*, however none were as highly abundant as the above. We also found significant within-season temporal variation in both plant community composition and all leaf traits other than δ13C and δ15N.

In regards to plant traits measured in this study, we found that variation of leaf thickness, LMA, and SWC is negligible, and these traits generally decrease as the season progresses. Conversely, differences in LDMC, RWC, and stomatal density vary substantially due to species identity and roofs. RWC in particular showed exceptionally high variation across the growing season, likely due to its high sensitivity to soil, atmospheric, and leaf-level environmental effects (Arndt et al. 2015). In addition, the close relationship between LDMC, stomatal density, and leaf nutrient traits (δ13C, δ15N, %C, %N, and C:N) with species identity suggest that the these traits may be useful tools in screening plant species for suitable use on green roofs, as these traits have close ties to drought tolerance and nutrient use (Barcelo and Poschenrieder 1990; Arndt et al. 2015).

In addition, overall positive linear relationships between traits suggest that these plants are maximizing drought tolerance (Bussotti and Pollastrini 2015). In essence, these plants share some similarity in traits with traditional *Sedum* plants used on green roofs. Specifically, LMA, LDMC, and leaf thickness relate directly to leaf construction, and their positive relationship to both measures of foliar water (RWC and SWC), suggest that plants with long-lived, tougher leaves capable of containing more water and are more resistant to desiccation (Edwards 2014). However, while the three highest abundance plant species follow this trend (increasing LDMC, LMA, and thickness), *P. tenuifolium* and *Schizachyrium scoparium* decrease in LDMC, LMA, and leaf thickness throughout the growing season meaning they are lighter, wider, and thinner. While greater leaf water content does not necessarily predict greater evaporative cooling (Blanusa et al. 2013), plant species capable of producing fewer leaves that are tougher and more drought tolerant could extend or enhance green roof cooling and storm-water retention properties by persisting through dry periods or extending activity later into the season.

Of particular concern in this study is the exceptionally high abundance of *Setaria faberi* and *Digittaria ciliaris* on these green roofs, as both are noxious weeds and invasive species in the United States (USDA, NRCS 2019). While the individuals on these green roofs may not be causing substantial harm to ecological or agricultural systems, they and other noxious weeds can increase maintenance costs through higher weed-removal effort and compete with more desirable plant species (Oberndorfer et al. 2007). Measurements of *S. faberi* in this study indicate that individuals on NYC green roofs are highly prolific, but have poor water retention qualities (low leaf thickness, RWC, and SWC). Similarly, a 2014 study comparing *S. faberi* and *D. ciliaris* (both of which were spontaneous in the green roofs in this study) found that *S. faberi* persisted later into the dryer months due to drought resistance (Itoh and Froud-Williams 2014). Because both of these species rank poorly in foliar water traits (Table S1), they should be considered for removal to enhance stormwater retention and evaporative cooling. Small, low-lying plants *Oxalis stricta* and *Euphorbia maculata* also rank poorly in terms of traits and may also be removed in favor of other low-lying species, such as *Stellaria media* (Fig. S2).

Interestingly, while many of the spontaneous plant species do not appear to rank highly in traits or green cover, *Oenothera biennis* (Onagraceae; Common Evening Primrose) and *Symphyotrichum pilosum* (Asteraceae; Frost Aster) do appear in the top 10 rankings. spontane *O. biennis* likely originated from the un-observed Diana Center green roof plots and inadvertently spread as scientists and students moved from green roof to green roof. Conversely, *S. pilosum* is entirely spontaneous with no known nearby source, and likely arrived through birds, wind, or personnel. While their green cover is relatively low, this may be due to the fact that both of these species were not planted directly into these plots at the inception of the green roofs. Regardless, both appear to be successful on green roofs with desirable qualities and should be considered for future use on other green roofs in this region.

Conclusion

Ecosystem service provision is a core motivator in the valuation and construction of any green infrastructure, however, these services can be sustained so long as the infrastructure continues to remain "green". In temperate climates like in NYC, plant communities change in accordance with the seasons and compounded changes in presence, abundance, and leaf traits in the green roof vegetation can have strong impacts on its function. In other words, some roofs will function better than others at different times of the year. To that end, this study finds that a suitable mixture of plant species for northeastern US urban green roofs include: *Pycnanthemum tenuifolium* (Lamiaceae), *Symphiotrichum leave, Symphiotrichum pilosum*, *Rudbeckia hirta*, *Solidago odora* (Asteraceae), *Panicum virgatum*, *Sorghastrum nutrans, Schizachyrium scoparium*, *Dichanthelium clandestinum*, *Deschampsia flexuosa* (Poaceae), and *Oenothera biennis* (Onagraceae) based on seasonal abundance and potential to contribute to ecosystem service provision as inferred by leaf traits. The invasive grass species *Setaria faberi* and *Digittaria ciliaris* should be removed and are discouraged from plantings due to poor abundance and leaf trait values. It is also important to note that, other factors such as the presence of nitrogen-fixers, rooting depth, attractiveness to pollinators, restoration targets, educational value, and aesthetic appeal are also important in species planting decisions (Oberndorfer et al. 2007). Further insights into the temporal dynamics of plant species on green roofs would benefit from direct, frequent quantitative measurement of physical parameters (i.e. incident light, albedo, temperature, wind speed, etc.) and ecophysiological measurements (i.e. stomatal conductance, photosynthetic rate, etc.) in order to characterize individual species performance in green roof ecosystem service provision.

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Author's contributions Eric Yee, Hilary Callahan, Kevin Griffin, and Matthew Palmer conceived and designed the study. Eric Yee and Sojin Lee carried out field observation, laboratory procedures, and data analysis. Eric Yee wrote the manuscript, and edited it with the assistance of Hillary Callahan, Kevin Griffin, and Matthew Palmer.

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Availability of data and material Upon publication, the data will be made available for use on the TRY Plant Trait Database.

Code availability Upon publication, the code will be made available for use on the TRY Plant Trait Database.

Declaration

Conflicts of interest We certify that we have no conflicts of interest regarding this work.

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