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Phylogenetic diversity and plant trait composition predict multiple ecosystem functions in green roofs

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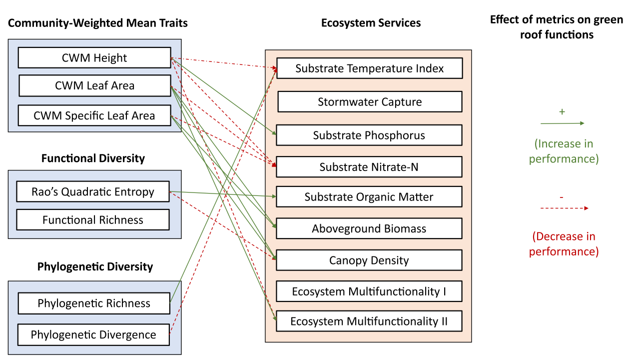
HIGHLIGHTS

- Functional/phylogenetic community structure provides mechanistic links to ecosystem services.
- We assessed multiple plant community metrics for different ecosystem services in green roofs.
- Functional traits of dominant plant species predicted multiple green roof services
- Functional diversity increased substrate organic matter on extensive green roofs
- Phylogenetic diversity and traits of dominant species predicted substrate cooling

GRAPHICAL ABSTRACT



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ABSTRACT

Plant selection and diversity can influence the provision of key ecosystem services in extensive green roofs. While species richness does predict ecosystem services, functional and phylogenetic community structure may provide a stronger mechanistic link to such services than species richness alone. In this study, we assessed the relationship between community-weighted trait values from four key leaf and canopy functional traits (plant height, leaf area, specific leaf area, dry leaf matter content), functional diversity, and phylogenetic diversity to ten different green roof functions, including ecosystem multifunctionality, in experimental polycultures. Functional traits of dominant plant species were a major driver for indicators of multiple green roof functions, such as substrate nitrate-N, substrate phosphorus, aboveground biomass and ecosystem multifunctionality. In contrast, functional diversity alone increased substrate organic matter. Moreover, both functional/phylogenetic diversity and identity predicted canopy density, substrate cooling. This study highlights the first line of evidence that distinct aspects of phylogenetic and functional diversity play a major role in predicting multiple green roof services. Therefore, we provide further evidence that to maximize green roof functioning, a very careful selection of plant traits and polycultures are needed.

1. Introduction

Green roofs provide several ecosystem services in urban environments (Dunnett and Kingsbury, 2004). Studies of green roof ecosystem services have prioritized roof temperature and heat flux moderation (Raji et al., 2015; Takakura et al., 2000), stormwater retention

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(Mentens et al., 2006; Stovin, 2010) and the provision of habitat for biodiversity (Williams et al., 2014). Extensive green roofs are characterized by shallow substrate, making it difficult to optimize any particular function due to limitations to plant biomass potential and species selection. This leads to a trade-off between the cost of increasing substrate thickness and the benefits of improved ecosystem function (Dusza et al., 2017; Feitosa and Wilkinson, 2016). Plant choice can influence the provision of many key services of extensive green roofs (Jim, 2015; Williams, 2015; Zhao et al., 2014) but laborious testing of hundreds of available plant species is logistically challenging. Consequently, ecologists have attempted to use species-level morphological and ecophysiological traits to predict performance of important ecosystem properties and services including drought tolerance (Lundholm et al., 2015), temperature moderation in hot (Monteiro et al., 2016; Williams, 2015) and cold seasons (Lundholm et al., 2014), stormwater capture (Farrell et al., 2013; Nagase and Dunnett, 2012; Starry et al., 2014), and nutrient uptake (Lundholm et al., 2015).

Green roofs provide a variety of services simultaneously, so it is not surprising that a single type of vegetation will not optimize all functions (Ranalli and Lundholm, 2008; Tanner, 1996). Testing the ability of plant species mixtures or polycultures (compared with monocultures) to improve single ecosystem services or increase multifunctionality on green roofs has been the focus of several studies (Cook-Patton and Bauerle, 2012; Dunnett et al., 2008; Franzaring et al., 2016; Johnson et al., 2016; Lundholm et al., 2010). Extensive green roofs have shown inconsistent effects of plant species diversity on ecosystem functions, with some showing better performance in species mixtures compared to monocultures (Johnson et al., 2016; Lundholm et al., 2010; Lundholm, 2015), and others showing equivalent or a reduction in performance (Dunnett et al., 2008; Franzaring et al., 2016; Nagase and Dunnett, 2012).

If a single function improves in a more species-rich community relative to a high-performing monoculture, this is referred to as mixture advantage (also transgressive overyielding or intercrop advantage (Trenbath, 1974; Vandermeer, 1981)). Mixture advantage has two potential mechanistic bases. The first is interspecific facilitation, whereby a species' contribution to the overall function of the system is enhanced when grown with another species (Kinzig et al., 2001). The second is niche complementarity (Kinzig et al., 2001) and occurs when two or more species, due to resource acquisition differences, can overall more fully exploit available resources, compared with monocultures, leading to enhanced functioning. Both mechanisms rely on species grown in mixtures being sufficiently different from one another in their functional traits, thus mixture advantage relies on functional diversity. However, the functional difference between species varies greatly, and so increasing species richness alone holds little guarantee of increasing functional diversity. Species-rich communities can also exhibit high levels of ecosystem functioning as they are more likely, by chance, to include individual species that drive function (selection or sampling effect: Loreau and Hector, 2001)). In constructed ecosystems, however, it is unlikely that designers will want to rely on chance in order to improve ecosystem function, so it is important to identify important functional traits that drive ecosystem functioning and determine whether combinations of species can reliably improve functioning.

Ecologists recognize many forms of functional diversity but to date, green roof studies have mainly emphasized taxonomic species richness or morphological life form diversity as indicators of plant diversity within species mixtures (Cook-Patton, 2015). If the species in a mixture are relatively similar, e.g. all succulents, then functional diversity in terms of the divergence of traits possessed by the species community may be low, despite high taxonomic (species) diversity. The calculation of functional diversity or dispersion relies on knowledge of functional traits of each plant species in a mixture (Schleuter et al., 2010). Various metrics have been proposed to quantify functional traits in ecological communities (Schleuter et al., 2010), which are chosen based on the given hypothesis and dataset. Another approach utilizes phylogenetic diversity, which refers to the degree to which species in a mixture are evolutionarily related to one another, and can serve as a proxy for functional diversity in cases where it is easier to obtain phylogenetic information on species compared with measured traits (Gerhold et al., 2015). Both functional and phylogenetic diversity measures are likely to be more closely related to ecosystem services in cases where facilitation or niche complementarity could increase ecological process rates. These approaches could be relevant to constructed and urban ecosystems (Dusza et al., 2017; MacIvor et al., 2016), but have not yet been used to evaluate the performance of extensive green roofs. Alternatively, it is possible that mean trait values of species mixtures are stronger drivers of ecosystem services than trait diversity. The mass-ratio hypothesis proposes that ecosystem functions will be driven mainly by traits shared by the dominant species in the mixture (i.e. functional identity), as opposed to their functional or phylogenetic diversity (Grime, 1998). Therefore, the goal of the current study is to evaluate functional and phylogenetic diversity indices and mean trait values as predictors of green roof ecosystem properties and services including biomass, substrate organic content, storm-water capture and substrate temperature reduction.

2. Methods

2.1. Study site

This study was conducted in the city of Halifax, Nova Scotia upon a single building approximately 5 m above the ground on Saint Mary's University campus in Halifax, Nova Scotia (446 399 N, 636 359 W). Extensive green roof modules were replicated in a full factorial design and complete details of the experimental setting and climate conditions during the study period can be found in (Lundholm et al., 2014, 2010). The original experiment was meant to test the relationships between species diversity and ecosystem functioning; the current study is a re-analysis of data collected during the original study (Lundholm et al., 2010, 2015). Modules were plastic freely-draining trays (36 cm × 36 cm × 12 cm) containing commercially available green roof substrate (Sopraflor X, Soprema Inc., Drummondville, QC, Canada) to a depth of 6 cm. Under the substrate layer, we placed an Enkamat (Colbond Inc., Enka, NC, USA) followed by a composite non-woven water retention mat (Huesker Inc., Charlotte, NC, USA).

2.2. Experimental design

In this study, we focus on species mixture treatments only (polycultures). Relationships between traits and ecosystem services in monocultures were the subject of a previous analysis (Lundholm et al., 2015). The plant communities within these green roof modules included a combination of three species each from five life-form groupings: tall forbs (*Campanula rotundifolia* L., *Plantago maritima* L., *Solidago bicolor* L.), succulents (*Sedum acre* L., *Sedum rosea* (L.) Scop., *Sedum spurium* M. Beib.), grasses (*Danthonia spicata* (L.) Beauv., *Deschampsia flexuosa* (L.) Trin., *Poa compressa* L.), creeping forbs (*Sagina procumbens* L. and two other species that disappeared from the study after year 1 (see Table 1 for more details). As a result, we do not include the creeping forb life-form group as it only contained a single species. However, three and five life-form treatments containing the creeping forb group (only *Sagina procumbens*) were analyzed. Each module was originally planted with 21 individuals. For the single life form treatment, seven individuals of each of three species in a particular group were planted, alternating individuals of different species to maximize potential interactions between species ($n = 5$ replicates for each life-form group treatment). For treatments comprised of three life-form groups, each combination of the three life-forms were tested ($n = 5$ replicates for each combination) with individuals of the requisite species added in random order until one of each was present, and then

Table 1
A description of species for monoculture and polyculture treatments. Abbreviations were for each species; creeping forbs: SAPR - *Sagina procumbens* L. (Sp); dwarf shrubs: EMNI - *Empetrum nigrum* L (En), GAPR - *Gaultheria procumbens* L. (Gp), VAVI- *Vaccinium vitis-idaea* (L. (Vv); grasses: DASP - *Danthonia spicata* (L.) Beauv.; DEFL - *Deschampsia flexuosa* (L.) Trin. (Df); POCO - *Poa compressa* (L.); succulents: SEAR - *Sedum acre* L. (Sa); SESP - *Sedum spurium* (M. Beib.); SERO - *Sedum rosea* (L.) Scop.; tall forbs: CARO - *Campanula rotundifolia* L. (Cr); PLMA - *Plantago maritima* L. (Pm); SOBI - *Solidago bicolor* L. (Sb). Highlighted cells indicate presence of a particular species within a green roof module.

	Species Pool List												
Treatment	CARO	PLMA	SOBI	SEAC	SERO	SESP	DASP	DEFL	POCO	SAPR	VAVI	GAPR	EMNI
D											x	x	x
G							x	x	x				
S				x	x	x							
T	x	x	x										
cts	x	x	x	x	x	x				x			
dcs				x	x	x				x	x	x	x
dct	x	x	x							x	x	x	
dgc							x	x	x	x	x	x	x
dgs				x	x	x	x	x	x		x	x	x
dgt	x	x	x	x	x	x					x	x	x
dts	x	x	x	x	x	x					x	x	x
gcs				x	x	x	x	x	x		x	x	x
gct	x	x	x				x	x	x	x			
gts	x	x	x	x	x	x	x	x	x				
cdgst	x	x	x	x	x	x	x	x	x	x	x	x	x

the pattern repeated until all 21 spaces were filled (Lundholm et al., 2010). A single treatment involving all species from all five life-forms was created ($n = 20$), with spaces filled as in the three life-form treatments. Finally, ten modules with substrate but no plants were established as controls. All modules were placed on a rooftop and grown for four years before the data used here were collected. There was no supplemental irrigation past the first month of the experiment, no fertilizers were added, and modules were weeded to remove species not planted in the corresponding treatment.

2.3. Ecosystem properties and services

We quantified indices of ecosystem functions in the fourth and final year of the experiment (Lundholm, 2015). Canopy density is the number of contact points with a pin frame, during the interval of peak aboveground biomass (# contacts with live plant parts/0.07 m^{-3}) (in August) and was correlated with winter and summer substrate temperatures in monocultures (Lundholm et al., 2015). Aboveground biomass was harvested after pin frame sampling and dried to a constant weight (Lundholm, 2015). At the same time, substrate was collected from each module and analyzed for organic matter, phosphorus and nitrate content (Lundholm, 2015). An index of stormwater capture was derived using a controlled water addition experiment by dividing the difference in module weight before and after watering (the amount of water retained) by retention values from unplanted control modules (MacIvor and Lundholm, 2011). An index of green roof cooling was calculated by taking substrate temperatures at solar noon twice during hot periods between July and August and dividing by the values from unplanted control modules then averaging for each module. This temperature index, and the phosphorus and nitrate values represent services where the lower the value, the greater benefit. Lower substrate temperatures are related to lower demand for air conditioning in summer. Lower phosphorus and nitrate values indicate less potential for negative impacts on water quality in roof runoff, so vegetation with higher uptake rates is more beneficial from this perspective. Two indices of multifunctionality were derived using summed values of the z-scores of individual service indicators (weighted equally) as described above, with temperature index, phosphorus and nitrate values multiplied by -1 to reflect that the lower values of the original variables indicate higher levels of the corresponding ecosystem service (Lundholm, 2015), index 1: stormwater index + ($-1 *$ temperature index); index 2: stormwater index + ($-1 *$ temperature index) + ($-1 *$ substrate P_2O_5 content) + ($-1 *$ substrate NO_3^-) + substrate organic content + aboveground biomass + canopy density.

2.4. Plant traits

Leaf and canopy traits were measured on all species used in the experiment using standard protocols (five mature leaves from five different individuals per species sampled in natural settings (Cornelissen et al., 2003; Lundholm et al., 2015): plant height, leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC). We calculated measures of functional diversity (FR) and phylogenetic diversity (PD) to determine relationships with measured ecosystem service indicators. We used realized species richness as a predictor variable in addition to the FR and PD measures as part of preliminary regression analysis (see below for more detail). Realized species richness was quantified in the final year of the experiment as the total number of plant species detected within a module. Average realized species richness was 2.5 in the single life form group treatments, 5 in the three-life form group treatments and 7 in the five-life form treatment, but varied both within and among life form treatments (Lundholm et al., 2014).

2.5. Functional diversity metrics

For this study, we chose community-weighted mean trait values (hereafter referred to as CWM) to examine how single traits contribute to the performance of green roof functions. CWM values were calculated for each trait by multiplying a given trait value (e.g. plant height in cm) by the proportional abundance (canopy density) of each species in each module (height: CWM H; leaf area: CWM LA; specific leaf area: CWM SLA; dry leaf matter content: CWM LDMC). While CWM represents the central tendency of the trait distribution of a given community, we used Rao's quadratic entropy as a complementary metric to represent the dispersion (and hence variance) of the four measured trait values in a multivariate trait space (Botta-Dukát, 2005). Further, we selected functional dendrogram-based richness (hereafter FR) as a functional equivalent to Faith's PD (see below), where we calculated FR from the principal component axes from all four log-transformed leaf traits and used UPGMA (Unweighted Pair Group Method with Arithmetic Mean) clustering as our hierarchical clustering method (Petchey and Gaston, 2006; Swenson, 2014). All functional diversity metrics were calculated from the dbFD function in the FD package in R (Laliberté and Legendre, 2010). All subsequent statistical and computational methods were performed in R v. 3.3.3 (R Core Development Team, 2016).

2.6. Phylogenetic diversity metrics

To construct the phylogeny, we first pruned eleven of our twelve species of interest from a mega-phylogeny in (Zanne et al., 2014), where the taxonomic classification was updated by (Qian and Jin, 2015), using the ape R package (Paradis et al., 2004). For the missing species, *Sedum* (*Rhodiola*) *rosea* was replaced with a congeneric proxy (*Rhodiola rhodantha*). Divergence times were estimated using Sanderson's penalized semiparametric likelihood method from the chronopl R package (Paradis et al., 2004; Sanderson, 2002) to create an ultrametric time-calibrated phylogenetic tree (see Fig. S1). A lambda parameter of 1000 was chosen based on the minimum value from a cross-validation approach.

For phylogenetic diversity metrics, we chose Faith's PD and the mean-pairwise phylogenetic distance (hereafter MPD). The reason for this choice of metrics was that different phylogenetic metrics are known to be sensitive to various topological aspects of a phylogenetic tree (e.g. imbalance of clades, "tippy" versus "stemmy") (Tucker et al., 2017). Thus, Faith's PD represents phylogenetic richness while MPD indicates phylogenetic divergence. Furthermore, Faith's PD tends to be correlated with species richness, which presents complications in subsequent statistical analysis due to a multicollinearity effect (see (Venail et al., 2015) for more details). Including MPD in our analyses provided orthogonal information about the phylogenetic structure of the green roof communities, as MPD is independent of species richness (Cadotte, 2015).

2.7. Statistical analyses

To determine if closely-related species have similar traits, we ran a phylogenetic signal test on all four traits (LA, SLA, LDMC and plant height) using Pagel's λ and Blomberg's K since they are known to be robust against branch length information. To test for significance, Blomberg's K and Pagel's λ were randomized 999 times to create a null distribution and then compared to observed values using the *phylosig* function in the phytools R package (Revell, 2012). For both test statistics, values close to zero indicate phylogenetic independence, and values close to one indicates that closely-related species tend to have similar traits assuming the trait variance follows a Brownian model of evolution.

We used general linear models in an information-theoretic (IT) framework to determine which set of phylogenetic and functional variables are correlated with seven different green roof ecosystem services and two different multifunctionality indices while accounting for model uncertainty and parsimony. Kendall's pairwise correlations revealed multicollinearity among the predictor variables (see Table 2). We removed CWM LDMC as a fixed variable from further statistical analyses to reduce any possible spurious results for the regression models (see (Dormann et al., 2013). Additionally, we ran a preliminary multiple regression analysis was performed to determine if there were any significant results among realized species richness, FR and PD for each ecosystem function, which revealed that species richness was a predictor in only one model (substrate nitrate-N content; Table S1). Therefore, we removed realized species richness as a fixed variable in subsequent statistical analysis to reduce any multicollinearity effects. All statistical models included CWM H, CWM LA, CWM SLA, MPD, FR, PD and Rao's Q as fixed predictor variables. We centered and standardized each predict variable to allow for a comparison of the relative amount of

Table 2
Kendall's rank correlation coefficient matrix of both community-weighted mean trait values for each plant trait (community-weighted mean height (CWM H), community-weighted mean leaf area (CWM LA), community-weighted mean specific leaf area (CWM SLA), community-weighted mean leaf dry matter content (CWM LDMC)) and community diversity measures (phylogenetic diversity (PD), mean pair-wise distance (MPD), functional richness (FR), functional diversity (Rao's Q)) for all experimental polycultures. Values indicate *tau* values. Significance is bolded (. marginal ($0.05 \le P \le 0.1$), $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

	MPD	PD	SR	Rao's Q	FR	CWM H	CWM LA	CWM SLA	CWM LDMC
MPD	–	**0.54*****	**0.55*****	**0.46*****	**0.53*****	0.00	0.02	**−0.21****	−0.02
PD	–	–	**0.84*****	**0.38*****	**0.83*****	**0.13**	**0.13**	**−0.15***	0.12
SR	–	–	–	**0.41*****	**0.91*****	0.10	0.09	−0.14	0.10
Rao's Q	–	–	–	–	**0.38*****	**0.44*****	**0.14***	**−0.13**	**0.38****
FR	–	–	–	–	–	0.08	0.10	−0.08	0.06
CWM H	–	–	–	–	–	–	**0.50*****	**−0.14***	**0.84*****
CWM LA	–	–	–	–	–	–	–	**0.27*****	**0.46*****
CWM SLA	–	–	–	–	–	–	–	–	**−0.18***
CWM LDMC	–	–	–	–	–	–	–	–	–

Table 3
A summary of how different biodiversity metrics affect the performance of multiple green roof service indicators. Red arrows indicate a decreased performance while green arrows indicate an increased performance. Abbreviations for each predictor variables are: phylogenetic diversity (PD), functional richness (FR), functional diversity (Rao's Q), mean pairwise distance (MPD), community-weighted mean height trait (CWM H), community-weighted mean trait specific leaf area (CWM SLA), and community-weighted mean leaf area (CWM LA).

	Predictor variables						
Green roof functions	PD	FR	Rao's Q	MPD	CWM H	CWM SLA	CWM LA
Soil organic matter	-	-	↗	-	-	-	-
Substrate phosphorus content	-	-	-	-	↗	-	-
Substrate nitrate-N content	-	-	-	-	↙	↙	↗
Aboveground biomass	-	-	-	-	-	↗	↗
Substrate temperature index	↗	-	-	↙	↙	-	-
Stormwater index	-	-	-	-	-	-	-
Canopy density	-	-	↙	-	-	↗	↗
Multifunctionality index 1	-	-	-	-	-	-	-
Multifunctionality index 2	-	-	-	-	↙	-	↗

variation explained by a single predictor while holding other independent variables constant in a given regression model (Schielzeth, 2010). In addition, we chose aboveground biomass, canopy density, substrate organic matter, substrate phosphorus content, substrate nitrogen content, stormwater retention, substrate temperature index and two multifunctionality indices as separate response variables for the regression models. Moreover, there was variation in the realized species richness among the experimental polyculture treatments. Under a similar IT framework, we compared general linear models for each response variable to linear mixed-effects models, where realized species richness was included as a random effect. The results were similar between both sets of models and thus we dropped realized species richness as a random effect in favor of the most parsimonious model. All linear mixed-effect models were fitted using maximum likelihood in the nlme R package (Pinheiro et al., 2013) and general linear models were fitted using the lm function in R.

We used an exploratory multi-model inference to determine the relative importance of predictor variables for various green roof ecosystem

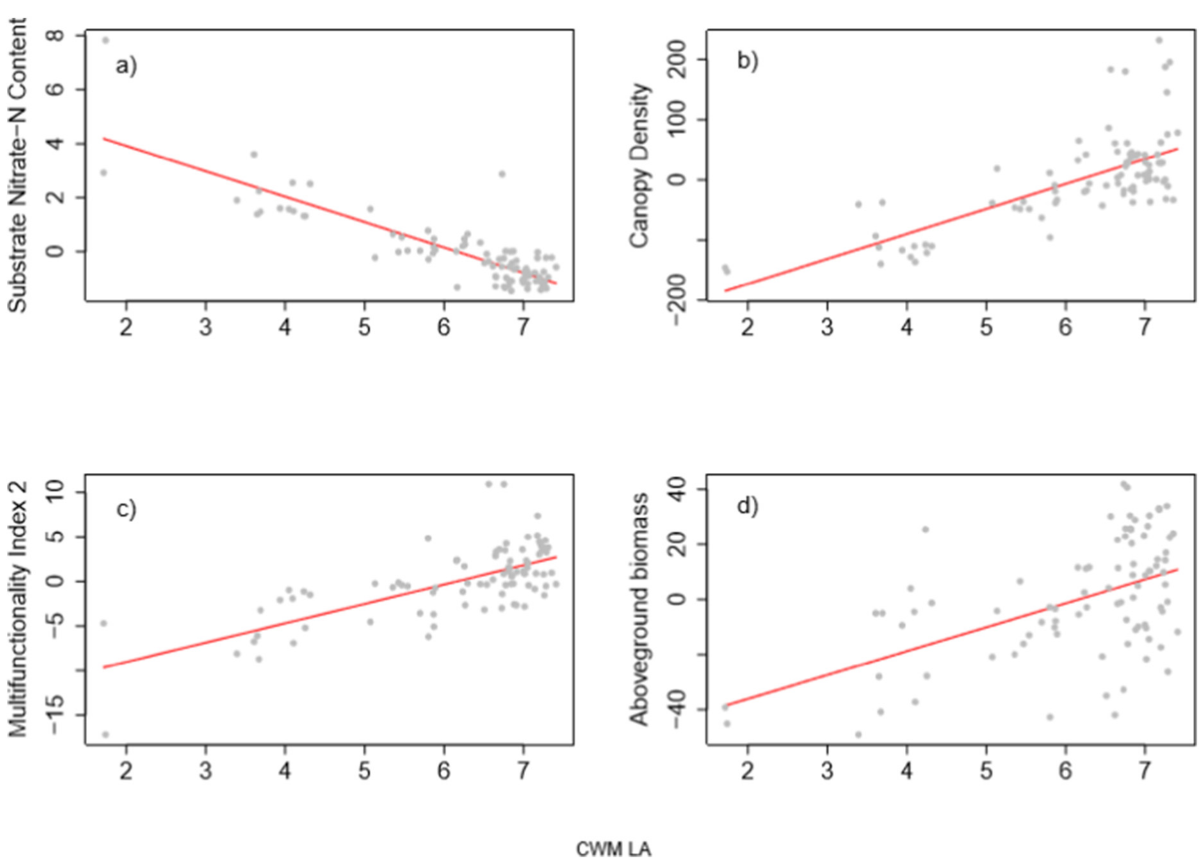

Fig. 1. Community-weighted mean LA predicts multiple ecosystem functions in green roofs. Partial residual plots of green roof functions and community-weighted mean leaf area for all experimental polycultures. Partial residuals of response variables (ecosystem services) are: (a) substrate nitrate-N, (b) canopy density (c) multifunctionality index 2 composed of all measured ecosystem functions in this study, and (d) aboveground biomass. A red line indicates significant linear relationships. See text for description of response variables. Abbreviations for predictor variables are: community-weighted mean leaf area (CWM LA).

services using information from all possible candidate models. = All seven predictor variables were combined to form $2^7 = 128$ models, including null models (intercept-only) and excluding interaction terms. Models were ranked according to decreasing values of the 'small sample size corrected version' of Akaike's information criterion (AICc) as a measure of the goodness of fit for each model. For each model, relative importance of predictor variables was calculated by the sum of the Akaike weights of all models containing a predictor variable. Using the 'natural averaging' approach, where insignificant predictor variables are not given a zero-value when performing model averaging, partial regression coefficients for each model were calculated as the Akaike-weighted conditional averages of coefficients from all models containing a particular term (Burnham and Anderson, 2003). We then re-evaluated each MuMIn model using linear regression models and significant predictor variables with high relative importance. We derived partial residual plots from each linear model using the "termplot" function in R to visually show the relationship between a predictor variable of interest and a given ecosystem function while accounting for the effects of other independent variables. Model ranking and inference were conducted in the MuMin R package (Bartoń, 2013) (Table 3).

3. Results

3.1. Community-weighted mean trait values

Community-weighted mean leaf area had a significant positive relationship with three green roof functions: aboveground biomass ($\beta = 0.59$, $w_i = 1.00$, $p = 0.001$), canopy density ($\beta = 0.57$, $w_i = 0.97$, $p < 0.01$), and multifunctionality index 2 ($\beta = 0.78$, $w_i = 1.00$, $p \leq 0.001$) (see Fig. 1b–d; Table S2). There was a negative relationship with substrate nitrogen content and CWM LA ($\beta = -1.28$, $w_i = 1.00$, $p = 0.001$) (see Fig. 1a; Table S2). Compared to CWM LA, CWM SLA showed positive relationships with three green roof functions: aboveground biomass ($\beta = 0.49$, $w_i = 1.00$, $p < 0.001$), canopy density ($\beta = 0.49$, $w_i = 1.00$, $p < 0.001$) and substrate nitrogen content ($\beta = 0.38$, $w_i = 0.99$, $p = 0.097$) (see Fig. 2a–c; Table S2). CWM H showed a significant positive relationship with substrate nitrogen content ($\beta = 1.03$, $w_i = 1.00$, $p < 0.001$), but was marginally significant with substrate phosphorus content ($\beta = 0.57$, $w_i = 0.88$, $p = 0.081$), and substrate temperature index ($\beta = 0.51$, $w_i = 0.93$, $p = 0.06$) (see Fig. 3a, d; Table S2). In contrast, CWM H was negatively correlated with multifunctionality index 2 ($\beta = -0.47$, $w_i = 0.80$, $p = 0.033$) (see Fig. 3b, Table S2).

3.2. Phylogenetic diversity and functional diversity

Plant height and SLA showed a significant phylogenetic signal in terms of Pagel's λ but not for LDMC and LA (see Table S3). Functional richness (FR), PD, MPD and Rao's Q were significantly higher in both the 9-species and 15-species polyculture treatment compared to the 3-species polyculture treatment (one-way ANOVA; FR: $F_{2,84} = 71.27$, $p < 0.001$; PD: $F_{2,84} = 85.56$, $p < 0.001$; MPD: $F_{2,84} = 33.68$, $p < 0.001$; RaoQ: $F_{2,84} = 16.66$, $p < 0.001$) (see Figs. S2–S5). The regression models illustrated that Rao's Q was only positively correlated with substrate organic matter ($\beta = 0.38$, $w_i = 0.91$, $p = 0.009$) (see Fig. 4b;

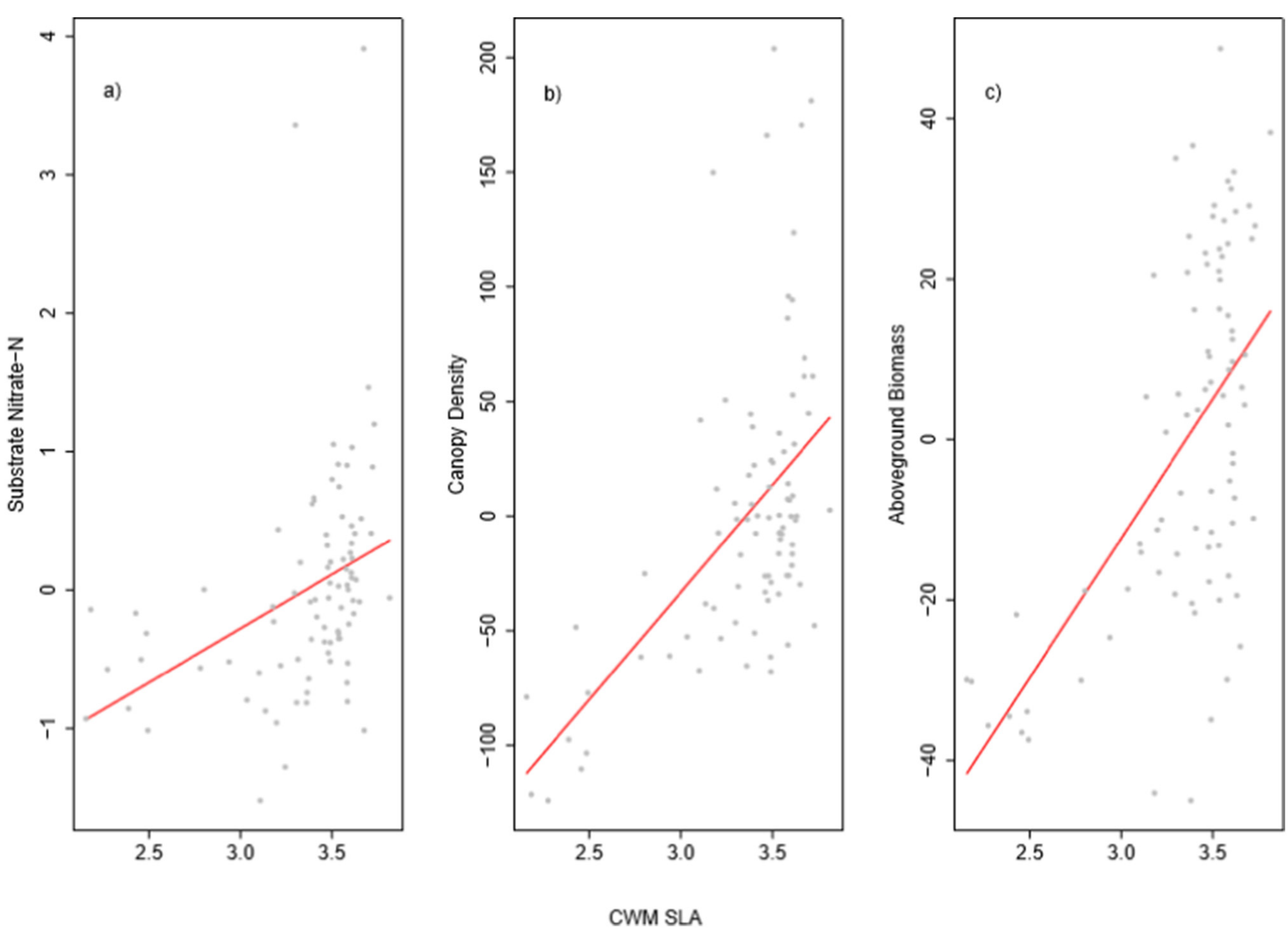

Fig. 2. Community-weighted mean SLA predicts multiple ecosystem functions in green roofs. Partial residual plots of green roof functions and community-weighted mean specific leaf area for all experimental polycultures. Partial residuals for response variables (ecosystem functions) are: (a) substrate nitrogen N, (b) canopy density, and (c) aboveground biomass. Red line indicates significant linear regressions. See text for description of response variables. Abbreviations for predictor variables are: community-weighted mean specific leaf area (CWM SLA).

Table S2). However, Rao's Q was negatively correlated with canopy density ($\beta = -0.31$, $w_i = 0.81$, $p = 0.031$) (see Fig. 4a; Table S2). PD was negatively correlated with the substrate temperature index ($\beta = -0.55$, $w_i = 0.86$, $p = 0.021$) while MPD had a higher marginal positive effect on substrate temperature index than PD ($\beta = 0.36$, $w_i = 0.86$, $p = 0.0773$) (see Fig. 4d,e). No diversity metric or community-weighted mean trait value had a significant effect on the multifunctionality index 1 (see Table S2).

4. Discussion

Previous studies on green roofs show that increasing species richness leads to improved performance of multiple green roof ecosystem functions (Lundholm, 2015). However, species richness per se may not offer ecologically meaningful information since both functional traits and/or phylogenetics may provide a stronger mechanism link to green roof functions through two opposing mechanisms: traits of dominant species and niche complementarity (Grime, 1998; Loreau and Hector, 2001). Here, our study represents a first attempt to examine how different functional and phylogenetic components of plant community structure (CWM H, CWM LA, CWM SLA, MPD, FR, PD, Rao's Q) in experimental green roof polycultures might predict important green roof ecosystem services.

4.1. Trait dispersion predicts a single green roof function

Trait dispersion was positively related to substrate organic matter content. Specifically, functionally dissimilar green roof communities resulted in higher carbon storage, possibly due to a combination of traits that vary in aboveground investments. In other words, green roof species with a greater range of trait values (e.g. SLA) drive increasing substrate carbon content. Since organic matter is a rough approximation of substrate carbon storage, this ecosystem property could be governed by two main processes - carbon exports and imports. As opposed to be driven by a single trait, substrate carbon storage in green roofs and other ecosystems is likely to driven by a combination of functionally diverse strategies related to litter decomposition (Garnier et al., 2016). Specifically, increased substrate carbon storage may be explained by increased primary production due to dominance of tall fast-growing plant species where the trade-off of short-life spans leads to a higher carbon input in the aboveground layer of a given green roof ecosystem through easily digestible litter content. Although, in this study there was no relationship between aboveground biomass and trait dispersion. Green roof polycultures may also consist of slow-growth species, which is reflected in low SLA, low height and high LDMC values. This set of species tends to conserve resources and nutrients, and hence may have high belowground biomass (De Deyn et al., 2008). This conservative strategy differs from that of fast-growth counterparts in that they can input low-quality plant material, which tends to result in slow decaying litter, and thus increased carbon input. Therefore, the combination of functionally diverse strategies may drive carbon input through varying litter quality. Alternatively, our findings could suggest that an increase in substrate organic matter is caused by a decrease in mineralization with functional diversity, as belowground biota may be slower to process the more chemically diverse litter produced by more functional diverse plant communities (Loreau, 2001).

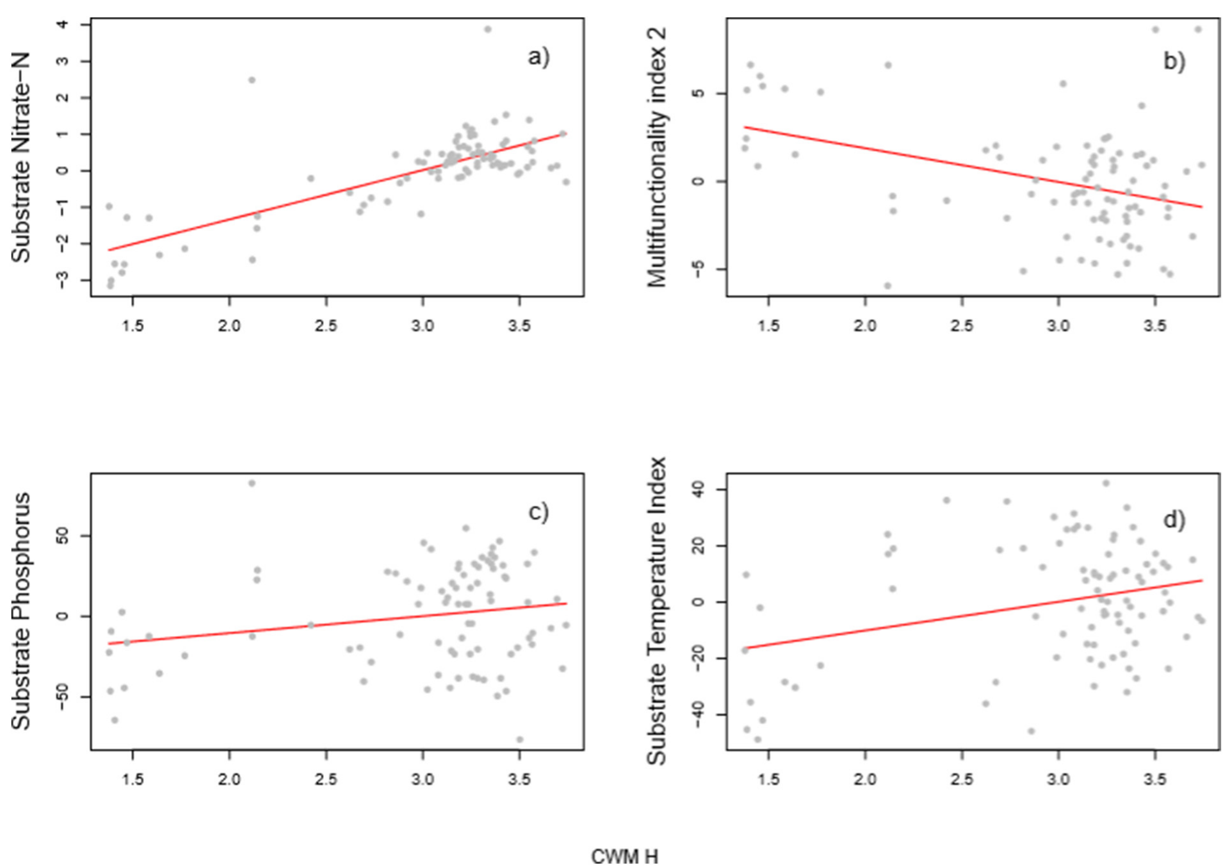

Fig. 3. Partial residual plots of green roof functions and community-weighted mean height for all experimental polycultures. Partial residuals of response variables (ecosystem functions) are: (a) substrate nitrogen N, (b) multifunctionality index 2, (c) substrate phosphorus and (d) substrate temperature index composed of all measured ecosystem functions in this study. Red line indicates significant linear regressions. See text for description of response variables. Abbreviations for predictor variables are: community-weighted mean specific leaf area (CWM H).

4.2. Both niche complementarity and mass-ratio effects influence green roof functions

In contrast, our results also show that both phylogenetic diversity and key traits of dominant species predict substrate cooling in green roofs despite having opposing mechanisms. Specifically, lower mean heights and higher phylogenetic richness were both associated with cooler substrate temperatures. The succulent life-form group was effective in reducing substrate temperatures during summer (Lundholm, 2015) and tended to be relatively short, but high phylogenetic diversity mixtures that included succulents and other plant groups also resulted in cool substrates. In other words, distantly-related plant species with short stature are associated with greater rooftop cooling. The impact of phylogenetic complementarity on green roof ecosystem services may also be partly due to temporal effects. Specifically, since the results come from the fourth and final year of a large-scale green roof experiment, the effect of complementarity may have increased over time, based on findings from other studies on both species-level diversity (Cardinale et al., 2007; Lundholm, 2015) and evolutionary relatedness (Cadotte et al., 2012). As such, higher PD values has been shown to increase primary productivity due to niche complementarity, as seen in other studies (Cadotte, 2013), which may in turn lead to higher rates of evapotranspiration and thus reduced substrate cooling. For example, phylogenetically diverse assemblages may result in the development of different rooting depths over time and consequently lead to differential use of substrate resources. However, our results suggest that both aboveground biomass and canopy density is driven by traits of dominant species rather than niche complementarity, suggesting that any changes in aboveground investments (e.g. through leaf traits) would have minimal influences on the relationship between PD and substrate cooling. Instead, the phylogenetic information among the local species pool might contain unmeasured traits linked to processes involved in substrate cooling such as belowground traits (Cadotte et al., 2013).

4.3. Traits of dominant green roof species impact ecosystem services

While both phylogenetic and trait diversity had some positive effects on green roof ecosystem services, our results reveal stronger support for the mass-ratio hypothesis; community mean trait values were better predictors than trait or phylogenetic diversity indices. Specifically, different combinations of community-weighted SLA, LA and height traits were correlated with green roof functions related to nutrient uptake (e.g. substrate phosphorus content, substrate nitrate-N content)) and ecosystem multifunctionality (e.g. multifunctionality index 2). The results suggest that the traits of dominant species are mainly responsible for influencing the ecosystem properties behind these green roof functions, rather than niche complementarity or facilitation linked to functional or phylogenetic diversity within the species mixtures.

For instance, high CWM SLA values may indicate a green roof composed of dominant plant species with fast-growth rates and high rates of resource acquisition, which are expected to be linked to primary productivity (Wright et al., 2004). In this study, CWM SLA was a predictor of both aboveground biomass and canopy density – metrics that act as a proxy for productivity, among the green roof polycultures, suggesting that the presence of highly-abundant green roof plant species (e.g. grasses) can have a great impact on productivity. Similar results were reported from monocultures (Lundholm et al., 2015) thus species mixture performance is responding to the same functional traits. Similarly, canopy density was positively associated with CWM SLA and CWM LA but negatively associated with Rao's Q, indicating the influence of a

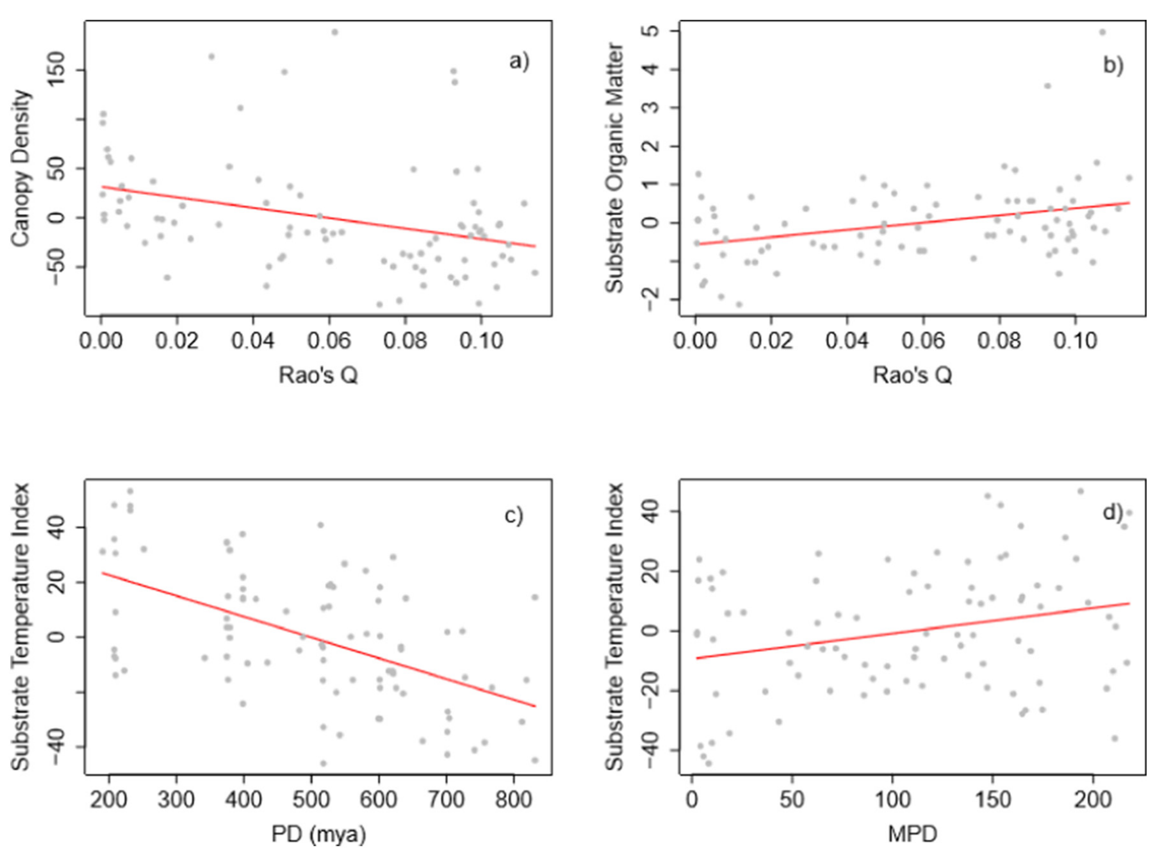

Fig. 4. Partial residual plots of green roof functions and community diversity metrics for all experimental polycultures. Partial residuals for response variables (ecosystem functions) are: (a) canopy density, (b) substrate organic matter, (c, d) substrate temperature index. See text for description of response variables. Abbreviations for predictor variables are: Rao's quadratic entropy (Rao's Q), Faith's phylogenetic diversity (PD), and mean pair-wise phylogenetic distance (MPD).

few fast-growing dominant green roof plant species (e.g. *Poa compressa* and *Deschampsia flexuosa*) that are functionally similar.

In addition, community-weighted mean trait values were predictors of phosphorus and nitrate-N substrate content, which lends further support to the mass-ratio hypothesis. Specifically, an increase in community-weighted mean height values lead to higher phosphorus uptake. As plant height is a general indicator of high growth rates (plant performance) and resource acquisition, communities with high CWM H should be composed of one of a few dominant plant species that rapidly acquire resources and thus possess nutrient-rich tissues. For instance, dominant plant species with such trait values could be *Sedum acre* and *Deschampia flexuosa*, and were previously shown to have high phosphorus uptake in green roof monocultures, and *Poa compressa* with high nitrate uptake (Lundholm, 2015). However, it must be emphasized that the nutrient values sampled were soil concentrations after four years of growth with a given vegetation treatment; low concentrations likely represent high uptake rates (as opposed to higher leaching rates) (Lundholm, 2015) but lower stocks of soil nutrients also represent a potential negative effect on future plant growth. More detailed nutrient budgeting is required in order to understand the relationships between plant communities and nutrient dynamics on green roofs (Johnson et al., 2016).

4.4. Study limitations

While the results do show that different facets of functional and phylogenetic diversity are important in predicting green roof functions, this study has substantial limitations. First, the original experimental design was intended to manipulate species richness alone, rather than functional or phylogenetic diversity. Future experiments should focus on disentangling the confounding of effects of species richness by creating an experimental gradient based on a functional/phylogenetic diversity metric that is uncorrelated with species richness (see (Dias et al., 2013). Second, our analysis to determine the multivariate trait space in this study is biased towards strictly leaf and canopy traits. As previously mentioned, belowground traits (e.g. root depth) may provide complementary information on the links between functional traits, functional diversity and green roof functions. Therefore, the incorporation of both key belowground and aboveground traits within a multivariate trait space might reveal stronger niche differences (Kraft et al., 2015) and possible reveal more links between niche complementarity and green roof functions.

5. Conclusions

The joint evaluation of functional diversity, phylogenetic diversity and community-weighted mean trait values is currently rare in the green roof literature. After controlling for species richness, it appears that traits of dominant green roof species mainly drive most of the green roof functions, including ecosystem multifunctionality, rather than niche complementarity or facilitation between functionally or phylogenetically diverse species. Meanwhile, functional diversity or phylogenetic divergence are relatively important in terms of both substrate cooling and substrate organic matter. This study provides potentially useful information for practitioners and managers in terms of plant selection for biodiverse green roofs (MacIvor et al., 2016).Therefore, careful consideration is needed to select which sets of traits are required to achieve a green roof function.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.02.093.

Competing interests

All authors declare no competing interests.

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