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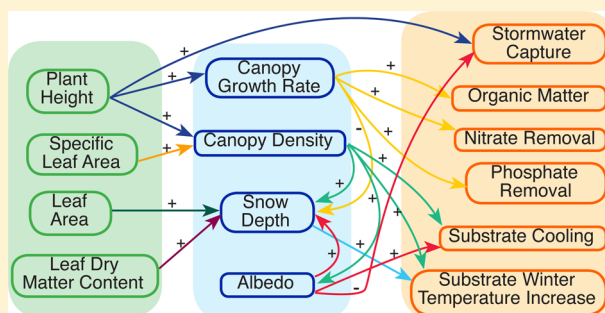
Plant Functional Traits Predict Green Roof Ecosystem Services

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S Supporting Information

ABSTRACT: Plants make important contributions to the services provided by engineered ecosystems such as green roofs. Ecologists use plant species traits as generic predictors of geographical distribution, interactions with other species, and ecosystem functioning, but this approach has been little used to optimize engineered ecosystems. Four plant species traits (height, individual leaf area, specific leaf area, and leaf dry matter content) were evaluated as predictors of ecosystem properties and services in a modular green roof system planted with 21 species. Six indicators of ecosystem services, incorporating thermal, hydrological, water quality, and carbon sequestration functions, were predicted by the four plant traits directly or indirectly via their effects on aggregate ecosystem properties, including canopy density and albedo. Species average height and specific leaf area were the most useful traits, predicting several services via effects on canopy density or growth rate. This study demonstrates that easily measured plant traits can be used to select species to optimize green roof performance across multiple key services.



INTRODUCTION

Constructed ecosystems such as treatment wetlands, green roofs, and biowalls are engineered to provide ecosystem services. These services depend on the presence of living plants and engineered components such as growing medium, membranes, and subsidies such as irrigation.^{1–3} Green roofs can reduce heat transfer through building roofs,⁴ retain stormwater,⁵ trap airborne particulate matter,⁶ sequester carbon,⁷ and provide habitat,⁸ amenity, and aesthetic values.³ Plant species and vegetation types differ in their ability to provide these services;³ thus, careful selection of plant species can optimize green roof functioning. Green roofs often feature extreme conditions relative to local natural ecosystems, including shallow soils and high winds; thus, plant selection is also important to ensure survival of green roof vegetation. There are thousands of plant species in each region that can be used on green roofs, yet screening all these would be logistically impossible; hence, there is a need for an efficient way to characterize plants based on general traits that predict their function in a green roof setting. Plant functional traits can be used to categorize species based on their effects on ecosystem processes.^{11,12} The plant trait approach highlights ecological function regardless of geographic distribution, taxonomic/phylogenetic relationships, and environmental niche and thus represents a general method to screen plant species for various purposes. Traits related to plant size and leaf morphology are relatively easy to measure, and relate to general plant strategies that differentiate species having evolved under different environmental conditions: plants that are shorter, with lower maximum growth rates, are typically found in areas with low soil fertility. These traits, in turn, can predict or influence ecosystem processes such as primary production, nutrient and water uptake, and transpiration rate^{10,11} but have

seldom been used in environmental engineering. For example, specific leaf area (SLA), leaf area/dry weight, tends to be higher for plants with relatively high growth rates, that inhabit relatively fertile areas. SLA can be considered a “soft” trait that does not directly drive ecosystem process rates but is correlated with variables more closely associated with function,¹¹ such as net photosynthetic capacity and maximum growth rate, which in turn can drive ecosystem productivity. Functional traits have been used recently in green roof studies to select plants appropriate for local climates,¹³ to predict growth rates,¹⁴ and to maximize survival and stormwater retention.¹⁵ This ecological approach uses traits measured in natural populations as indicators of generic plant strategies and employs these traits to predict ecosystem functions in different situations. The current study is the first to undertake a comprehensive analysis of the relationships between multiple ecosystem services provided by green roofs and generic plant traits.

METHODS AND MATERIALS

The green roof site was on the Saint Mary's University campus, approximately five meters above ground level and circumscribed by buildings one to three stories higher on all sides (Appendix S1, Supporting Information). The climate of Halifax is cold, humid, and maritime (Appendix S1). We used measurements of ecosystem properties and services from two previously established experiments in the same modular green roof system, comparing species grown in monoculture in the

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78 same growing medium on the same site.^{14,16–18} Plant species
79 were selected from harsh environments that have similarities to
80 green roofs (Appendix S1). Experiment 1 involved the estab-
81 lishment of 13 species in 2007,^{14,16} three modules per species
82 ($n = 3$) (Table 1) (planting details in Appendix S1). Each
83 replicate module was a black plastic nursery tray (36 cm \times
84 36 cm \times 12 cm), with a free-draining base, lined with a
85 composite nonwoven water-retention layer (Huesker Inc.,
86 Charlotte, NC), followed by an Enkamat (Colbond Inc.,
87 Enka, NC) drainage/filter layer which was topped with growing
88 medium (Sopraflor X, Soprema Inc., Drummondville, QC,
89 Canada) to a depth of approximately 6 cm (above the
90 Enkamat).¹⁶ All modules were weeded throughout the experi-
91 ment to remove volunteer species.

92 Canopy density, considered an “ecosystem property” here
93 (number of contacts with live plant parts/0.07 m³), was
94 determined in each module using a three-dimensional pin
95 frame (36 cm \times 36 cm \times 36 cm) with 16 pins. The total
96 number of contacts between live plant parts and the pins was
97 recorded, and data from the 2010 biomass peak (taken in
98 August). Canopy growth rate incorporated canopy density
99 measurements at the end of the growing season (August) in
100 year 1 (2007) and year 2 (2008) to calculate the change in
101 density as a rate, relative to initial density: $\ln(\text{density at } t_2) -$
102 $\ln(\text{density at } t_1)/\text{number of days between } t_1 \text{ and } t_2$. Albedo was
103 quantified by placing modules one-by-one on a gray colored
104 weed barrier fabric (Quest Plastics Ltd., Mississauga, ON,
105 Canada). A single LI-COR pyranometer sensor and LI-250A
106 light meter (LI-COR Biosciences, Lincoln, NE) was affixed to
107 a retort stand, with the sensor and light meter 35 cm above
108 the upper edge of the module. Under clear sky conditions
109 within 1 h of solar noon incoming and reflected radiation were
110 measured in August 2010, within 1 week of canopy density
111 sampling. Incoming radiation (W/m²) was measured by
112 directing the pyranometer sensor toward the sky (180° away
113 from the module), and reflected solar radiation was measured
114 by facing the sensor directly at the module surface. These are
115 relative measurements with validity only within our green roof
116 system and were taken to compare relative reflectivity of the
117 different plant species in monoculture (Appendix S1).

118 An index of water loss rate was derived from water addition
119 experiments during the growing season of 2010: modules were
120 weighed using a PX-Series Checkweighing bench scale (ATRON
121 Systems Inc., West Caldwell, NJ), 1.3 L of water was added to
122 the substrate (representing a medium-sized rain event for the
123 region, equivalent to 10 mm of rain), by slowly pouring the water
124 at the base of the vegetation layer, slowly moving the container
125 so that the water would end up equally distributed across the
126 surface. Modules were reweighed 10 min later to determine
127 “stormwater capture” as the difference between pre- and
128 postwatering weights, twice between June–August. Modules
129 were reweighed 24 and 48 h later with the difference between
130 postwatering weights and weights 24 or 48 h later used as an
131 index of water loss (Appendix S1). These experiments were
132 carried out on sunny days within 1 h of solar noon. Ten
133 unplanted control modules were established and integrated with
134 the planted modules at the start of the experiment in 2007
135 (Appendix S1). Indices of relative water capture and loss were
136 created for each planted module each time the experiment was
137 performed by dividing the planted module value by the average
138 of the control (unplanted) modules in the same block.

139 Indicators of ecosystem services were quantified during the
140 2010 growing season. The effect of vegetation on substrate

temperatures during summer indicates a cooling service: lower
substrate temperatures are linearly correlated with lower net
heat flux into the building.¹⁶ To create an index that can be
used to compare vegetation at different times with variation in
ambient air temperatures and insolation, we calculated an index
of relative cooling by dividing the substrate temperatures in
planted modules within 1 h of solar noon on a sunny day¹⁶
(once in May, once in July) by the average substrate
temperature of the control modules in the same block at the
same time (measurement details in Appendix S1). Three
variables related to soil chemistry services were calculated for
experiment 1. Growing medium samples (250 mL per module,
Appendix S1) were collected at the end of the growing season
(September 2010) and assessed for organic matter content
(%)(loss on ignition), nitrate-N (ion-specific electrode), and
phosphate (P₂O₅) (Mehlich 3 extraction, inductively coupled
argon plasma), and were again converted to indices of relative
content by dividing planted module values by the average
value of control modules in the same block. Organic matter
content was included as an index of the ability of green roof
vegetation to increase carbon storage over time;⁷ soil nutrient
concentrations were included, as greater nutrient uptake by the
vegetation may be associated with higher runoff water quality,¹⁹
so lower nutrient concentrations were assessed as indicating
higher performance of nutrient removal services.

In 2009 we set up experiment 2, involving 10 replicates each
of 12 species and an unplanted control using the same modular
system as the previous experiment^{17,18} (four of these species
were also in experiment 1) (Appendix S1). Canopy growth
rate was determined for the first two years of growth as in the
other experiment. Substrate temperature was measured in the
same way as in experiment 1 during the same growing season
(2010) in May, July, and August. The stormwater capture
trials were performed three times between June–August 2010.
Snow depth was quantified as it impacts substrate temperature
and heat flux in winter and is affected by vegetation.¹⁸ As an
ecosystem property, we used average snow depths when
there was snow coverage from January 7–March 7, 2011
(Appendix S1). As experiment 1 was harvested and soil
nutrients quantified at the end of the growing season in 2010,
we could only examine winter performance for experiment 2.
Snow depths were used to represent the general effect of the
species monocultures on the differential accumulation of snow
on the substrate surface. In winter, net heat flux out of the
building is negatively correlated with substrate temperature,¹⁸
so we used the minimum substrate temperature recorded be-
tween November 5, 2010, and March 31, 2011 (Appendix S1)
and divided by the average minimum of the control modules in
the same block as an index of “heat trapping” in winter (higher
minima represent less heat lost in the winter). The experiment
2 modules were used in a subsequent experiment so substrate
was not extracted and analyzed for nutrients and organic matter.

For indices that were measured more than once, we used the
temporal average for each module. We then took an average of
all modules of that species for each variable representing an
ecosystem property or ecosystem service for use in multiple
regression analyses. Indicators of ecosystem services for
which lower values indicate greater performance (e.g., a lower
substrate temperature in summer indicates greater cooling
ability of the vegetation, so replicates with cooler substrates
registered low indices relative to controls) were first reflected
(multiplied by -1) so that higher performance would register
as a higher value. This was performed for the “substrate

Table 1. Measured Plant Traits, Ecosystem Properties, and Ecosystem Service Indicators (means \pm standard error)

| species ^a | growth form | height (cm) ^b | leaf area (mm ²) | specific leaf area (mm ² /mg) | leaf dry matter content (mg/g _{fresh weight}) | canopy growth rate ((contacts _{T2} - contacts _{T1})/growing season days) | albedo index | canopy density (leaf contacts/0.07m ³) | water loss index | stormwater capture index | substrate cooling index ^c | organic matter index ^d | phosphate index | nitrate index | substrate winter temperature increase index | snow depth index |
|---|-------------------------|--------------------------|------------------------------|--|---|---|-----------------|--|------------------|--------------------------|--------------------------------------|-----------------------------------|-----------------|----------------|---|------------------|
| <i>Arctostaphylos uva-ursi</i> (expt 1) | creeping shrub | 6 \pm 1 | 128.5 \pm 16.6 | 5.9 \pm 0.5 | 444.7 \pm 7.3 | $6.5 \times 10^{-4} \pm 1.1 \times 10^{-4}$ | 0.17 \pm 0 | 22 \pm 12 | 0.95 \pm 0.0 | 1.03 \pm 0.0 | 1.02 \pm 0.0 | | | | 0.97 \pm 0.0 | 0.96 \pm 0.1 |
| <i>Symphotrichum novi-belgii</i> (expt 2) | tall forb | 54 \pm 5 | 1062.5 \pm 220.8 | 23 \pm 1.4 | 195.6 \pm 6 | $3.8 \times 10^{-3} \pm 4.4 \times 10^{-4}$ | 0.2 \pm 0.0 | 55 \pm 9 | 1.22 \pm 0.1 | 1.04 \pm 0.0 | 0.88 \pm 0.0 | | | | 1.12 \pm 0.0 | 0.91 \pm 0.11 |
| <i>Campanula rotundifolia</i> (expt 1) | tall forb | 16 \pm 3 | 102.2 \pm 23.9 | 16.3 \pm 1.8 | 262 \pm 22.1 | $3.3 \times 10^{-3} \pm 1.3 \times 10^{-3}$ | 0.19 \pm 0 | 110 \pm 5 | 1.04 \pm 0.1 | 0.96 \pm 0.0 | 0.8 \pm 0.0 | 1.09 \pm 0.0 | 0.87 \pm 0.1 | 0.2 \pm 0.1 | | |
| <i>Carex argyrantha</i> (expt 2) | sod forming graminoid | 63 \pm 0 | 1451.1 \pm 137 | 35.3 \pm 4.8 | 580.8 \pm 27.4 | $8.2 \times 10^{-4} \pm 8.7 \times 10^{-4}$ | 0.2 \pm 0.01 | 163 \pm 25 | 1.14 \pm 0.0 | 1.04 \pm 0.0 | 0.8 \pm 0.0 | | | | 0.81 \pm 0.1 | 1.39 \pm 0.2 |
| <i>Carex nigra</i> (expt 2) | sod forming graminoid | 67 \pm 3 | 1116.1 \pm 141.4 | 10.5 \pm 0.9 | 401.2 \pm 23.5 | $9.4 \times 10^{-4} \pm 1.4 \times 10^{-4}$ | 0.2 \pm 0.0 | 154 \pm 20 | 1.10 \pm 0.0 | 1 \pm 0.0 | 0.82 \pm 0.0 | | | | 0.7 \pm 0.0 | 1.34 \pm 0.1 |
| <i>Danthonia spicata</i> (expts 1 and 2) | bunch forming graminoid | 36 \pm 2 | 90.2 \pm 10.8 | 9.5 \pm 1 | 402.8 \pm 46.6 | $1.1 \times 10^{-3} \pm 3.8 \times 10^{-4}$ | 0.18 \pm 0 | 121 \pm 13 | 0.87 \pm 0.0 | 0.99 \pm 0.0 | 0.85 \pm 0.0 | 0.95 \pm 0.1 | 1.11 \pm 0.2 | 0.48 \pm 0.2 | 0.67 \pm 0.0 | 1.16 \pm 0.1 |
| <i>Deschampsia flexuosa</i> (expts 1 and 2) | bunch forming graminoid | 57 \pm 2 | 81.8 \pm 13.2 | 13.3 \pm 2.2 | 368.8 \pm 45.9 | $1.7 \times 10^{-3} \pm 4.4 \times 10^{-4}$ | 0.17 \pm 0 | 98 \pm 15 | 0.95 \pm 0.0 | 1.01 \pm 0.0 | 0.9 \pm 0.0 | 1.07 \pm 0.1 | 0.84 \pm 0.1 | 0.85 \pm 0.2 | 0.9 \pm 0.1 | 0.98 \pm 0.1 |
| <i>Empetrum nigrum</i> (expts 1 and 2) | creeping shrub | 8 \pm 1 | 4.6 \pm 0.4 | 40.1 \pm 3.1 | 90.2 \pm 20.8 | $1.7 \times 10^{-4} \pm 4.5 \times 10^{-4}$ | 0.17 \pm 0.01 | 56 \pm 10 | 0.91 \pm 0.0 | 1.07 \pm 0.0 | 0.94 \pm 0.0 | 0.95 \pm 0.1 | 1.13 \pm 0.1 | 0.46 \pm 0.3 | 0.92 \pm 0.0 | 0.94 \pm 0.1 |
| <i>Festuca rubra</i> (expt 2) | sod forming graminoid | 55 \pm 6 | 141.1 \pm 26.6 | 16.1 \pm 4 | 303.5 \pm 38.8 | $1.3 \times 10^{-3} \pm 1.5 \times 10^{-3}$ | 0.18 \pm 0.0 | 243 \pm 38 | 1.02 \pm 0.0 | 1.11 \pm 0.0 | 0.85 \pm 0.0 | | | | 0.68 \pm 0.0 | 1.46 \pm 0.1 |
| <i>Gaultheria procumbens</i> (expt 1) | creeping shrub | 10 \pm 1 | 357.8 \pm 38.4 | 7.3 \pm 0.5 | 382.9 \pm 10.1 | $-2.7 \times 10^{-3} \pm 1.3 \times 10^{-3}$ | 0.16 \pm 0 | 5 \pm 4 | 1.11 \pm 0.1 | 1.04 \pm 0.0 | 0.95 \pm 0.0 | 0.99 \pm 0.2 | 1.15 \pm 0.2 | 0.89 \pm 0.3 | | |
| <i>Plantago maritima</i> (expt 1) | tall forb | 14 \pm 2 | 228.7 \pm 81.2 | 7.3 \pm 0.6 | 112.6 \pm 6.5 | $1.3 \times 10^{-3} \pm 4.3 \times 10^{-4}$ | 0.17 \pm 0 | 47 \pm 7 | 0.87 \pm 0.1 | 1.01 \pm 0.0 | 0.88 \pm 0.0 | 1.24 \pm 0.2 | 0.92 \pm 0.2 | 0.32 \pm 0.1 | | |
| <i>Poa compressa</i> (expt 1) | sod forming graminoid | 26 \pm 6 | 1662.0 \pm 465.0 | 41.8 \pm 6.9 | 244.8 \pm 57.3 | $3.4 \times 10^{-3} \pm 6.8 \times 10^{-4}$ | 0.19 \pm 0 | 209 \pm 60 | 0.92 \pm 0.1 | 1.01 \pm 0.0 | 0.74 \pm 0.0 | 0.99 \pm 0.1 | 1.09 \pm 0.2 | 0.1 \pm 0.0 | | |
| <i>Sagina procumbens</i> (expt 1) | creeping forb | 2 \pm 0 | 16.5 \pm 4.0 | 92.4 \pm 23.3 | 167 \pm 19.5 | $-2.7 \times 10^{-3} \pm 5.1 \times 10^{-4}$ | 0.18 \pm 0 | 101 \pm 8 | 1.10 \pm 0.1 | 0.95 \pm 0.0 | 0.86 \pm 0.1 | 1.01 \pm 0.1 | 1.17 \pm 0.2 | 0.83 \pm 0.4 | | |
| <i>Sedum acre</i> (expt 1) | succulent | 4 \pm 0 | 18.5 \pm 2.8 | 37.0 \pm 8.4 | 124.7 \pm 13.6 | $1.4 \times 10^{-3} \pm 5.1 \times 10^{-4}$ | 0.26 \pm 0.0 | 124 \pm 30 | 1.07 \pm 0.1 | 0.87 \pm 0.0 | 0.74 \pm 0.0 | 1.13 \pm 0.2 | 0.78 \pm 0.1 | 0.87 \pm 0.3 | | |
| <i>Rhodiola rosea</i> (expt 1) | succulent | 18 \pm 0 | 152.8 \pm 36.0 | 16.9 \pm 1.1 | 85.4 \pm 4.9 | $-2.7 \times 10^{-3} \pm 1.0 \times 10^{-3}$ | 0.16 \pm 0 | 22 \pm 6 | 0.96 \pm 0.0 | 0.96 \pm 0.0 | 0.94 \pm 0.0 | 0.92 \pm 0.1 | 1.18 \pm 0.2 | 1.25 \pm 0.9 | | |
| <i>Sedum spurium</i> (expt 1) | succulent | 5 \pm 1 | 162.9 \pm 11.8 | 30.0 \pm 3.2 | 86.7 \pm 5.5 | $-8.5 \times 10^{-4} \pm 1.5 \times 10^{-3}$ | 0.21 \pm 0 | 87 \pm 39 | 0.84 \pm 0.1 | 0.93 \pm 0.0 | 0.8 \pm 0.0 | 0.93 \pm 0.1 | 1.11 \pm 0.2 | 0.35 \pm 0.1 | | |

Table 1. continued

| species ^a | growth form | height (cm) ^b | leaf area (mm ²) | specific leaf area (mm ² /mg) | leaf dry matter content (mg/g _{fresh weight}) | canopy growth rate ((contacts _{T2} - contacts _{T1})/growing season days) | albedo index | canopy density (leaf contacts/0.07m ²) | water loss index | stormwater capture index | substrate cooling index ^c | organic matter index ^d | phosphate index | nitrate index | substrate winter temperature increase index | snow depth index |
|---|----------------|--------------------------|------------------------------|--|---|---|--------------|--|------------------|--------------------------|--------------------------------------|-----------------------------------|-----------------|---------------|---|------------------|
| <i>Sibbaldopsis tridentata</i> (expt 2) | creeping shrub | 9 ± 3 | 395.6 ± 108.3 | 8.1 ± 0.3 | 380.9 ± 6.8 | -3.4 × 10 ⁻³ ± 1.8 × 10 ⁻³ | 0.17 ± 0.0 | 40 ± 15 | 1.02 ± 0.0 | 1.07 ± 0.0 | 0.92 ± 0.0 | | | | 0.92 ± 0.0 | 1.12 ± 0.1 |
| <i>Solidago bicolor</i> (expts 1 and 2) | tall forb | 29 ± 3 | 653.8 ± 222.2 | 8.0 ± 0.6 | 267.8 ± 12.9 | 2.5 × 10 ⁻³ ± 5.7 × 10 ⁻⁴ | 0.2 ± 0.0 | 58 ± 18 | 0.95 ± 0.0 | 1.03 ± 0.0 | 0.89 ± 0.0 | 1.16 ± 0.1 | 0.97 ± 0.1 | 0.14 ± 0.0 | 1.04 ± 0.0 | 1.05 ± 0.1 |
| <i>Solidago puberula</i> (expt 2) | tall forb | 41 ± 3 | 705.5 ± 75.1 | 28.4 ± 2.9 | 448.4 ± 24.5 | 2.2 × 10 ⁻³ ± 7.1 × 10 ⁻⁴ | 0.2 ± 0.0 | 55 ± 15 | 0.94 ± 0.0 | 1.06 ± 0.0 | 0.93 ± 0.0 | | | | 0.99 ± 0.0 | 1.08 ± 0.1 |
| <i>Vaccinium macrocarpon</i> (expt 2) | creeping shrub | 8 ± 1 | 26.0 ± 2.3 | 7.3 ± 0.6 | 582.6 ± 17.2 | -1.4 × 10 ⁻³ ± 8.5 × 10 ⁻⁴ | 0.18 ± 0.01 | 14 ± 4 | 0.9 ± 0.0 | 1.04 ± 0.0 | 0.99 ± 0.0 | | | | 0.96 ± 0.1 | 0.99 ± 0.1 |
| <i>Vaccinium vitis-idaea</i> (expt 1) | creeping shrub | 4 ± 0 | 56.2 ± 7.6 | 6.2 ± 0.4 | 465.4 ± 9.1 | -3.1 × 10 ⁻³ ± 8.9 × 10 ⁻⁴ | 0.16 ± 0.01 | 0 ± 0 | 1.11 ± 0.1 | 0.97 ± 0.0 | 0.97 ± 0.0 | 0.85 ± 0.1 | 1.29 ± 0.2 | 1.12 ± 0.4 | | |

^aNomenclature follows.²⁵ ^bTrait data (height, SLA, leaf area, and LDMC) for experiment 1 are from the literature.¹⁴ ^cSeveral variables were reflected in analyses (cooling, phosphate, nitrate, winter temperature increase); hence, low values in this table represent high performance of desired functions. ^dSoil chemistry data were only collected from experiment 1; winter data (snow depths and substrate winter temperatures) were only collected for experiment 2.

cooling”, “substrate winter temperature increase”, phosphate, and nitrate “removal” indices (Appendix S1).

Plant traits are usually measured on plants growing in typical environmental conditions in field settings, so that trait values are representative of natural populations.²⁰ To determine plant traits for each species used in these experiments, five leaf samples per species were obtained from different individuals growing in their natural habitats (Appendix S1). Following established protocols,^{11,20} healthy, fully expanded leaves from well developed plants were selected (Appendix S1). Within 2 h of collection fresh weight was measured and the five leaves per species scanned. Leaves were dried at 50 °C for 48 h and dry weight was measured. From these measurements, the following traits were obtained for the 21 test species: plant height, leaf area (LA), specific leaf area (SLA), and leaf dry matter content (LDMC). Plant height was determined as the average height of the five plants sampled in the field (to the nearest mm). LA was determined from the average of the five leaves, by measuring the one-sided surface area of the scanned image of each individual leaf using ImageJ software (version 1.47; NIH, USA) (Appendix S1). SLA was calculated as one-sided leaf area divided by its oven-dried weight, in mm²/mg. LDMC is the measure of dry leaf weight (mg) divided by fresh leaf weight (g).

We evaluated the relationships between plant species traits, monoculture ecosystem properties, and ecosystem service indicators using multiple linear regression in order to construct a path diagram. We first evaluated the relationships between ecosystem properties and service indicators (model results in Table S1, Supporting Information) and then the relationships between plant traits and ecosystem properties. As we hypothesized that plant traits affect ecosystem services via differences in ecosystem properties, we only examined the direct effects of plant traits on ecosystem services if there were no adequate models linking ecosystem properties directly to services. Variables were transformed to improve homogeneity of variance, and standardized (Z-scores)²¹ (Table S1). Model fit was evaluated using the AICc criterion.²² All models were compared using delta-weights, and when multiple models had delta-weights lower than 7,²³ model averaging was used to generate standardized regression coefficients (Table S1). The path diagram was constructed using only those coefficients whose 95% confidence limits did not overlap zero. Model selection and averaging procedures used the MuMIn package in R.²⁴

RESULTS AND DISCUSSION

Measured traits differed greatly among species with leaf area spanning more than 3 orders of magnitude (Table 1). Leaf area was highest in sod-forming graminoids but highly variable within that group, relatively high in bunch-forming graminoids, and lower but highly variable within the other growth forms (Table 1). Height was consistently low in creeping forbs and shrubs, relatively low but highly variable within the succulents, and high but variable within a growth form for the grasses and tall forbs. Leaf dry matter content (LDMC) showed the least variation with an almost 7-fold difference between the lowest and highest species values (Table 1). Low LDMC species included all the succulents and *Empetrum nigrum*, *Plantago maritima*, and *Sagina procumbens* (each from a different growth form group). Specific leaf area (SLA) tended to be low for creeping shrubs, except for *E. nigrum*. SLA for other growth forms varied greatly within a group. *S. procumbens*, the only creeping forb included, had the highest SLA (Table 1).

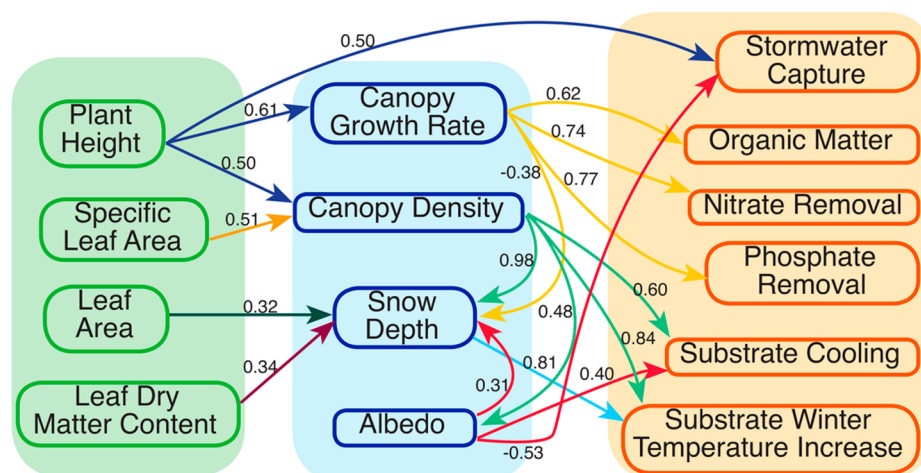


Figure 1. Relationships between plant traits (left), green roof ecosystem properties (center), and indicators of ecosystem services (right). Standardized regression coefficients determined by model averaging (showing only relationships with coefficients whose 95% confidence intervals did not overlap zero).

Measured ecosystem properties also differed across growth forms and species. Growth rates were slightly negative for *S. procumbens*, *Gaultheria procumbens*, *Sibbaldiopsis tridentata*, *Vaccinium macrocarpon*, *V. vitis-idaea*, *Rhodiola rosea*, and *Sedum spurium* (Table 1). These are species that generally inhabit extremely shallow and low-nutrient soils²⁶ and are expected to have low growth rates. These results also indicate that the canopies produced by these species reached their approximate maximum densities in the green roof system by the end of the first growing seasons. Tall forbs had consistently high canopy growth rates, as did both groups of grasses (Table 1). The succulent *S. acre* also had a relatively high growth rate. Creeping shrubs and forbs had low positive or negative canopy growth rates. The index of albedo showed the greatest range of variation within the succulent group with both the lowest and highest values (~16% reflectivity for *R. rosea* and ~26% for *Sedum acre*). Species in the other groups varied much less (between 16% and 19% reflectivity). Canopy density ranged from zero (for the extremely short ground cover *V. vitis-idaea*) to 243 contacts/0.07m³ for the sod-forming graminoid *Festuca rubra*. Grasses tended to have consistently high canopy density, whereas tall forbs had consistently intermediate values (Table 1). While all creeping shrubs were at the low end of canopy densities, there was considerable variation among species in the group, as well as in the succulent group. Water loss rates ranged from ~16% lower than unplanted controls (*S. spurium*), implying that the vegetation blocked evaporation from the bare substrate (relative to controls) but also had very low transpiration rates, to 22% higher (*S. novi-belgii*) than controls. Values substantially lower than controls were found in other species (*Danthonia spicata*, *E. nigrum*, and *V. macrocarpon*) that tended to concentrate their leaf biomass close to the substrate surface, likely presenting a barrier to evaporation from the substrate surface. There was otherwise little consistency in water loss within a growth form group. The effect of the planted species on snow depths ranged from 46% higher than unvegetated control modules in the dense-canopied *F. rubra* and other sod-forming graminoids, to close to no difference from controls for sparse-canopied tall forb *Symphotrichum qnovi-belgii*, and some creeping shrubs (Table 1).

Consistent with other green roof studies,²⁷ vegetation had a relatively small effect on stormwater capture, with the greatest

increase relative to controls around 10% for *F. rubra* (Table 1). Creeping shrubs tended to be at the high end for stormwater capture, along with tall forbs, with succulents at the low end. Several species had lower capture than controls (*S. acre* had one of the lowest). Vegetation reduced summer substrate temperatures up to 26% lower than controls (*Poa compressa* and *S. acre* had the coolest substrate). Some species were very similar in substrate temperature to controls (*Arctostaphylos uva-ursi*, *V. macrocarpon*, *V. vitis-idaea*). In general, creeping shrubs tended to cool the substrate the least, followed by tall forbs, with inconsistent results among grass species and highly variable performance among the succulents (Table 1). Organic matter showed little difference from controls, with high variability within a species and no consistent patterns between growth forms, save that the three tall forb species tended to have relatively high amounts of organic matter. Most species contained equivalent phosphate in their substrate to controls; the only species standing out with relatively low phosphate were *S. acre* and *Deschampsia flexuosa*. Substrate nitrate varied greatly among species with *P. compressa* showing very low levels (10% of the control values), considerable range among the three grass species, consistently low values among the three tall forbs, and no clear pattern among the other species (Table 1). Most species increased minimum winter substrate temperatures (registering as lower values in Table 1) relative to controls. Two grasses with relatively dense canopies close to the ground (*D. spicata* and *F. rubra*) raised winter minimum temperatures by approximately 30% relative to controls (Table 1). Grasses tended to have the highest winter minimum temperatures, whereas tall forbs and creeping shrubs had similar values to controls.

Most of the ecosystem service indicators were predicted by vegetation properties (Figure 1). Stormwater capture was positively correlated with plant height but not any of the vegetation properties. The index of water loss rate was not predicted by plant traits and did not predict any of the services. The three services related to substrate chemistry (organic matter, phosphate, and nitrate removal) were all positively predicted by canopy growth rate, which was positively predicted by plant height (Figure 1; Table S1). Substrate cooling was positively related to albedo and canopy density. Albedo was also related to canopy density but not any of the plant traits. Canopy density was positively related to both SLA

and plant height. Substrate winter temperature increase was positively correlated with snow depth and canopy density. Deeper snow was associated with denser canopies, lower canopy growth rates, and higher albedo. Leaf area and LDMC were also positive predictors of snow depth.

Plant traits represent general characteristics of plant species, but their effects on ecosystem processes are mediated through canopy characteristics and the effects of plant canopies on microclimates.^{28–30} In this study, “ecosystem properties” represent empirically measured canopy variables from monoculture species populations grown in the green roof setting. Traits related to overall plant size and leaf characteristics measured under natural conditions predicted canopy density, canopy growth rate, and snow depth, which in turn predicted the ecosystem service indicators. The plant traits used as predictors here represent easy-to-measure “soft”²⁰ traits that are correlated with process rates but not necessarily closely related mechanistically to ecological processes.

Plant height is a general indicator of high growth rates and/or evolution in resource-rich environments where competition for light is important, although there are many trade-offs involved in growing tall.³¹ The tallest species in this study were primarily graminoids and tall forbs (Table 1), which are associated with deeper soils and more fertile conditions, and had higher growth rates in the green roof system. It is important to note that “height” and the other leaf traits are general indicators of the fertility of the habitats where the species tend to grow naturally. While taller species performed some ecosystem services more effectively than shorter species in this system, there are important caveats relevant to interpreting these results. First, the species selected for these experiments all grow in relatively harsh or resource-limited environments (Appendix S1) and tend to be relatively short compared with species from more fertile habitats. Our finding implies that the species that are tallest in a set of short species perform these services better than the shorter ones. Second, while the species we grew on the green roof generally grew shorter than under natural conditions, there may be disadvantages for relatively tall species in green roof environments. Relatively tall species may be more susceptible to drought,³² and tall species from relatively fertile environments may have higher resource requirements leading to population crashes if fertilization or supplemental irrigation are not applied. This study ran for a relatively short period of time so longer studies are required to determine how height and long-term survival may be related.

Stormwater capture was positively related to plant species height, possibly due to an overall greater resource demand and water uptake, possibly mediated through greater root biomass, which supports what has been found in other studies.^{33,34} In this study, species height also predicted canopy growth rate, and density, which were positive correlates of all the ecosystem service indicators except stormwater capture.

Canopy growth rate relates to the overall primary production of a population of a given species and is expected to be correlated with the organic matter content of soils,³⁵ and rates of nutrient uptake.³⁶ Here canopy growth rate was a relatively strong predictor of all three services related to soil properties: organic matter, phosphate, and nitrate contents. Species from relatively fertile environments (indicated by taller heights) grew faster in the green roof system and resulted in higher substrate organic matter, and lower phosphate and nitrate contents, likely as a result of overall higher rates of multiple metabolic processes.

Canopy density represents the density of live leaf and stem parts in aboveground vegetation and was higher in the green roof system for species that were generally taller in their natural environments and had higher SLA values. These species, in turn, gave rise to lower summer substrate temperatures and higher winter minima. SLA represents the amount of investment in light-intercepting area per unit of dry mass and is expected to be higher in species from more resource-rich environments, resulting in a higher ability to harvest light per unit biomass allocation.³⁷ Again it is important to emphasize that the high SLA species in this study are generally from the most fertile areas in low productivity areas (coastal barrens, rock outcrops) that have some similarities with the green roof environment (shallow substrates, exposure to wind and sun). SLA is positively correlated with net photosynthetic capacity,³⁸ potential growth rate,³⁹ and evapotranspiration rate.⁴⁰ High SLA species in this study belong to a greater diversity of growth forms than tall species: forbs, graminoids, shrubs, and succulents were all among the highest SLA species.

High LDMC species included two dwarf shrubs in the same genus (*Vaccinium*); low LDMC species were the succulents, *E. nigrum* and *Plantago maritima*, which have relatively thick leaves and likely high water storage similar to the true succulents. Species with large individual leaf area included some graminoids and tall forbs. Both leaf area and LDMC were weak positive predictors of snow depth, although canopy density had the strongest effect of any of the individual variables. This shows that dense canopies led to greater trapping of windborne snow, accumulation of less dense snow, and/or decreases in melt rate, as predicted in previous work.¹⁸ When canopy density is held constant there were also independent effects of leaf area and LDMC so species with larger individual leaves and/or greater dry matter content also resulted in deeper snow layers which have a moderating effect on winter substrate temperatures (Figure 1). While we did not measure canopy density in the winter (i.e., we used August canopy densities to predict snow depths in the following winter) the strong predictive power of summer canopy density implies that species with dense canopies in summer retain dense canopies of dead stems and leaves or woody tissue in winter. Some of the high canopy density species tested in the snow study were relatively slow growing; thus, there was a negative relationship between growth rate and snow depth. The relationships between snow accumulation and plant traits are complex, as snow accumulation represents the outcome of several distinct processes.⁴¹ Canopy density had an effect on raising minimum winter substrate temperatures independent of snow depth, suggesting that plant residues, leaves from evergreen species, or other structures helped retain heat in the substrate. One possible mechanism is the reduction of convective heat losses due to reduction of air movement within the canopy⁴² and lower wind speeds at ground level⁴³ even when canopy material is largely dead.

Here we used an ecological approach to predict green roof services: plant traits measured on plants growing in their natural habitats were linked to ecosystem services via statistical models, using empirical data from replicated green roof modules. The approach taken by environmental engineers usually involves using numerical models of physical processes to predict key variables, and altering parameter values to explore sensitivity to environmental variability due to climate or vegetation type.⁴ The finding that substrate cooling has a positive relationship with both albedo and canopy density is congruent with the findings from numerical heat balance models, although our temperature

index includes several sources of variation from averaging across replicates within a species and sampling dates. Parametric variations in simulation studies have found leaf area index (LAI, representing single-sided total leaf area in the canopy) to be one of the most important parameters in determining the reduction of substrate surface temperatures, with LAI inversely related to substrate surface temperature.^{44–46} This result is due to LAI being a factor in the calculation of convective heat transfer, evapotranspiration, and shading. These heat fluxes are generally calculated according to the “big leaf” approach, i.e., the Penman–Monteith equation for evapotranspiration, whereby the heat fluxes of a single, average leaf are extrapolated to the canopy level via the LAI. While we did not measure LAI directly, within a species, LAI and canopy density should be linearly and positively related. Further empirical work to quantify LAI for different green roof vegetation types is the next step to link screening of species using ecological traits with prediction of green roof functioning.

Sensitivity analyses suggest that plant height is one of the primary variables determining thermal gain through green roofs.⁴⁷ In this study, average plant height for a given species in its natural habitats is correlated with substrate cooling via its role in canopy density (Figure 1), possibly via greater reflection and/or absorption of solar radiation, represented in numerical models by the extinction coefficient. Plants that were relatively tall in natural habitats produced a lot of canopy density on the green roof, due to high productivity and a generally taller stature than the other species. However, the role of plant height in reducing ground heat flux is also likely due to its role in the aerodynamic resistance of convective and latent heat transfer. According to the logarithmic wind profile approach adopted in numerous green roof heat balance models,^{4,48,49} vertical wind shear within the canopy increases the convective and evapotranspiration heat losses from the green roof system for taller plants by reducing the aerodynamic resistance and thus reducing the heat flux into the substrate. Thus, taller plants likely influence substrate temperatures via several mechanisms simultaneously.

Additional cooling mechanisms reduce the importance of albedo in the surface energy balance of a green roof compared to a conventional roof;⁵⁰ however, the results of this study showed canopy albedo still had a positive relationship with substrate cooling. To simulate the effects of albedo on heating loads, one study compared *Sedum tomentosum* in monoculture to a mixture of *Sedum* species,⁵¹ which had measured canopy reflection coefficients of 0.23 and 0.11, respectively, using a previously validated green roof model.⁵² The average peak net radiation difference and average net radiation between the two plant conditions was as high as ~16% and ~20%, respectively, suggesting that plant screening for canopy albedo may result in improvements to green roof thermal performance. None of the plant traits we used predicted albedo, so additional traits related to leaf optical properties would need to be incorporated to allow this kind of screening.

Several empirical studies show that stormwater retention in green roofs is related to antecedent soil moisture content;^{5,27,53} thus, high transpiration rates in the vegetation should be able to increase the water holding capacity of soil. While some green roof studies show a relationship between water loss rate and stormwater capture,¹⁶ the current study did not show this. The index of water loss used here represented water lost within the first 48 h of water addition, when conditions were wet and water loss would be a function of both evaporation from

substrate surface and transpiration from the canopy, as well as possible drainage after the first 10 min of runoff. A longer drying period, leading to a drier substrate surface, might have produced a clearer signal of differential transpiration rates among species and a stronger effect on subsequent stormwater retention, as evaporation from the substrate surface would have been minimized after it dried out completely. Stormwater capture should be a function of water loss over the entire interval between rain events; thus, the experimental method employed here likely overlooked the differences among plant species in ET rates over the longer term.

Since leachate from green roofs can be high in nutrients,^{53,54} the uptake and retention of nutrients by vegetation could mitigate nutrient pollution in runoff. Here we measured substrate concentrations of nitrate and phosphate after four years of plant growth; the index of removal was relative to control modules in which leaching was presumed to be the primary process driving nutrient loss. The low nutrient content relative to controls in some plant species treatments (Table 1) suggests that plant uptake and cycling within the plant–substrate system is responsible for the reductions, rather than greatly increased leaching rates for vegetated modules. We did not quantify leachate concentrations directly, and it is clear that further work needs to be done to examine the effects of plant species on nutrient dynamics and water quality in green roof systems. Likewise, our measurement of organic matter is intended to be an index of the differential ability of plant species to contribute toward carbon capture in the system, although it omits key variables such as inorganic carbon that are essential to understand the entire impact of green roof vegetation on carbon sequestration.⁷ These indices only partially capture the important ecosystem services of green roofs, but they clearly respond to differences in plant species, suggesting that plant traits can be used to optimize ecosystem service provisioning.

While shallow-substrate (extensive) green roofs are usually planted with succulents due to their superior drought tolerance, the plants with the highest trait values tended not to be succulents in this study. The most common vegetation for shallow-substrate green roofs is mixtures of *Sedum* species or other succulents.⁹ While here we only quantified the effects of plant traits on monoculture provisioning of ecosystem services, a past study on the same system showed that a *Sedum* mixture and *S. acre* monocultures performed similarly for summer substrate temperature reductions, albedo, and stormwater capture (other services were not quantified).¹⁶ This suggests that *Sedum* mixtures should be effective at summer cooling but relatively poor in stormwater capture, relative to other species we examined. As several other studies have shown,^{16,33,35,55,56} succulents are not always the best choice if particular ecosystem services are to be optimized besides roof cooling, but less drought tolerant species sharing the traits identified here could be included on green roofs depending on regional climate, availability of irrigation, and other factors.

In addition to *Sedum* mixtures, shallow-substrate green roofs often employ more diverse species and growth form mixtures.⁸ Some designs feature multiple species planted as monocultural beds, and our results are relevant to single-species patches within diverse roofs of this kind. However, predicting ecosystem services from species-diverse roofs featuring multispecies communities requires a different approach. Future studies should examine functional trait diversity in species mixtures to determine the effects on ecosystem services. The approach we

adopted allows prediction of monoculture performance as a first step toward screening lists of species for possible inclusion in mixed plantings.

This study also shows that broad growth form groupings can exhibit considerable variation in traits among species, suggesting that functional traits, rather than growth form groups might be used for green roof plant selection. Height and SLA were the best predictors, and while height was consistent for only some of the growth form groups, SLA was highly variable both within and between groups. Out of the species tested here, we could recommend designing green roofs with species that have relatively high SLA and height values, such as *F. rubra*. It is also possible that mixtures of species with opposite trait values (e.g., a short species with high SLA such as *S. procumbens* and a tall species such as *Carex nigra* with low SLA) might be combined to yield optimal functioning, if the diversity in morphology leads to complementary resource use or other synergistic effects.¹⁶ However, the design criteria for a particular roof, including ecosystem services to be maximized, may require attention to other traits not measured here such as flowering period or other variables related to habitat use by animals or human aesthetic criteria.

This study used plant leaf and traits determined by an average of measurements from plants from five naturally occurring populations. The ecosystem properties and service indicators measured on the green roof also represent averages within each species. Despite the considerable variation in traits and response variables within a species (Table 1), there was still a high predictive ability across species. The novelty of this study is to show that simple leaf and canopy traits can predict multiple important green roof functions. While the indices we used cannot be directly converted into precise estimates of ecosystem services for use in cost benefit analyses or use in numerical modeling, traits can be used to screen large numbers of species. Plant traits for many regional floras are now available in databases⁵⁷ and can be used to generate plant lists for further empirical testing and for the design of many kinds of constructed ecosystems.

■ ASSOCIATED CONTENT

■ Supporting Information

Appendix S1: Detailed methods. Table S1: Multiple linear regression models used for construction of path diagram in Figure 1. This material is available free of charge via the Internet at <http://pubs.acs.org>.

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The manuscript was written through contributions of all authors. All authors have given approval to the final version of the manuscript.

■ Notes

The authors declare no competing financial interest.

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■ ABBREVIATIONS

| | |
|------|-------------------------|
| SLA | specific leaf area |
| LDMC | leaf dry matter content |
| LAI | leaf area index |
| ET | evapotranspiration |

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