Green roofs as urban habitat for native plant seedlings and wild bees

By

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Abstract

Though green roofs offer an integrated response to urban issues, no designs that promote seedling survival and diversity have been investigated, and few studies have quantified the relationship between green roof resources and invertebrate visitors. Research presented here has two objectives: to determine the effect of designed heterogeneity on substrate conditions and seedling dynamics of green roofs, and to compare the composition and pollen collecting habits of bee communities visiting green roof, urban, and coastal barrens habitat. Several features cooled substrate, retained substrate moisture, increased seedling survival, and delayed species loss in periods of drought. Relative to ground level habitats, green roof wild bee communities were less abundant and species rich but shared species with all habitat types. Pollen collection of bumblebees on green roofs was similar to that observed in urban and barrens habitat. These results suggest that green roofs may offer harmonized solutions to multiple urban problems.

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Chapter 1

Introduction: “Green roofs as urban habitat for native seedlings and wild bees”

Introduction

Horizontal and vertical surface impermeability, large human populations, and significant disturbance of historical habitat states characterize modern cities. By 2030, the total area of urban land use is projected to swell by 1.2 million km^2 relative to estimates for 2000 (Seto et al. 2012). Management of environmental challenges related to urbanization, such as municipal stormwater treatment and climate control of buildings, can be costly (Clark et al. 2008). In addition, local flora and fauna can be affected by habitat loss; through fragmentation or disturbance, they may no longer have access to suitable habitat within the city (Grimm et al. 2008; McKinney 2006; Seto et al. 2012). Some of these affected organisms may contribute key services themselves, such as pollination, decomposition, or pest control (Hole 1981; Lowenstein et al. 2015; Raupp et al. 2010). Ecosystem services, the beneficial services provided by natural systems to humans, include processes as diverse as stormwater filtration and capture, climate control, decomposition, erosion reduction, and pollution abatement. Green roofs, or rooftops equipped with the materials necessary to grow plants, can mitigate some of the negative impacts associated with urbanization by providing multiple ecosystem services, including stormwater capture, thermal regulation, sequestration of pollutants, and habitat provisioning, that benefit both humans and non-humans (Oberndorfer et al. 2007).

Modern green roofs were designed in Germany in the 1970s with the intention of integrating and improving rooftop functionality (Köhler, 2004; Oberndorfer et al., 2007). Early work focused on reducing rooftop flammability and modulating building temperature (Köhler 2004; Kolb & Schwarz 1986), but many more ecosystem services have since been described. These services include stormwater capture, which involves both a reduction of runoff volume and a delay in peak runoff, pollution abatement, energy conservation, and urban heat island management (Getter & Rowe 2006; Oberndorfer et al., 2007). Although specific ecosystem services can be provided by alternative means (e.g. the increased albedo of white roofs has a cooling effect (Rosenzweig et al. 2006); trees in urban parks effectively store carbon (Nowak & Crane, 2002)), green roofs can simultaneously optimize multiple ecosystem functions and expand the total area of urban green space without compromising plans for ground-level development.

Green roof design

There are two main forms of green roofs, extensive and intensive, which are categorized by substrate or soil depth. Deep intensive green roofs feature substrate depths exceeding 20 cm, whereas shallow extensive green roofs feature a maximum substrate depth of 20 cm (FLL 2008). Substrate depth influences overall green roof weight, moisture availability, rooting depth, and heat flux - all of which impact provisioning of ecosystem services and plant species suitability (Liu & Baskaran, 2005). While intensive green roofs can support diverse plant assemblages and can provide significant benefits to building owners (Mentens et al. 2006), they are costly and often maintenance-intensive. Therefore, extensive green roofs, which also provide ecosystem services but are less expensive to install and can be retrofitted onto a rooftop, are more popular for building owners to install (Clark et al. 2008).

The choice of an extensive or intensive roof is one of many factors that can modify the delivery of ecosystem services by a specific green roof. Substrate composition determines porosity and permeability, which will alter stormwater capture and insulation value (Ampim et al 2010). The substrate colour will modify its albedo, which influences the thermal performance of the roof (Liu & Baskaran, 2005). Roof height and proximity to other buildings will govern airflow and solar exposure (Buckland-Nicks et al. 2016), which influence thermal and hydrological properties. And, importantly, the size of the green roof footprint will influence the scale of benefits provided.

Green roof vegetation

In addition to the abiotic characteristics of a green roof, the composition of its vegetation layer can affect the delivery of individual or combined ecosystem services (Cook-Patton & Bauerle 2012). Lundholm (2015) found that combinations of plant life-forms enhanced individual services such as temperature regulation, stormwater retention, nutrient uptake, and carbon sequestration, while also increasing green roof performance as measured by two indices of multi-functionality. However, outside of the recent work by Lundholm, research describing the provisioning of ecosystem services by green roofs has been conducted on roofs populated by a mix of species within a single genus of succulent plants (*Sedum*) (Gaffin et al. 2006; Getter & Rowe 2006; Mentens et al. 2006; Oberndorfer et al. 2007; vanWoert et al. 2005).

These low-maintenance succulents are cold-hardy and reliably green in the face of prolonged drought, making them the preferred plants for vegetating roofs (Dunnett & Kingsbury 2004; Snodgrass 2005), though significant differences in gas exchange characteristics, and, thus, ecosystem service provisioning, have been identified among species of *Sedum* (Starry et al. 2014). Early green roof cultivation trials that broke from industry tradition by using native plant species of varying life-forms suffered from inadequate species selection criteria and an underestimation of the disparity between ground-level and rooftop growing conditions (Monterusso et al. 2005; Dvorak & Volder 2010; Butler et al. 2012).

Given the demonstrated effect of vegetation composition on the performance of green roofs (Lundholm et al. 2010; Lundholm 2015; Van Mechelen et al. 2015), design approaches that foster the creation and maintenance of diverse plantings should be prioritized. Enhancement of plant diversity may be achieved through informed plant selection and physical modification of roof conditions. One successful green roof plant-selection approach involves the identification of habitats that feature growing conditions analogous to those present on a green roof (Lundholm 2006; Sutton et al. 2012; Van Mechelen et al. 2014). Plants growing in these analogous environments are likely to be pre-adapted to harsh green roof conditions, so species selected from these environments should perform well on green roofs. In Nova Scotia, several successful candidate green roof plant species have been identified from coastal barrens habitat (MacIvor et al. 2011; MacIvor & Lundholm 2011b; Wolf & Lundholm 2008). Coastal barrens are open habitats dominated by ericaceous plant species; they feature high light intensities, high wind speeds, and variable soil moisture conditions (Porter 2013), similar to a green roof environment. Within coastal barrens, habitat microsites and their associated plant communities can be quite variable (Cameron & Bondrup-Nielsen 2013; Oberndorfer & Lundholm 2009; Porter 2013), and even those microsites that are not water limited can yield suitable green roof candidate species (Wolf & Lundholm 2008). Other template habitats that have contributed to successful green roof native plant palettes elsewhere in North America include alvars, limestone barrens, cliffs, shortgrass prairies, and dry alpine environments (Bousselot et al 2011; Natvik 2008; Sutton et al 2012; Thuring 2007).

Green roof faunal communities

Beyond plant selection, maintenance of diversity in green roof plant assemblages may be achieved though manipulations of physical roof characteristics, such as water availability, shading, substrate type and depth, or the presence of surface features. Some “biodiverse roofs” have been installed in Europe with the intention of increasing the heterogeneity of the green roof environment (Brenneisen 2003; Brenneisen 2006; Köhler & Poll 2010; Bousselot et al. 2013); “brown roofs” are a version of biodiverse roofs that seek to emulate brownfield habitat, a type of abandoned urban green space known to provide valuable habitat to flora and fauna (Bates et al. 2013). Features often integrated into biodiverse roof designs include re-located ground-level soil, native plants, heterogeneity of substrate depth and composition, surface features, and recycled or reclaimed substrate materials (Ampim et al. 2010; Brenneisen 2006; Molineux et al. 2009).

The majority of green roofs feature an engineered growing medium that is homogeneous in depth and composition. This profile produces minimal microsite diversity, increasing the likelihood of establishing a non-diverse plant community (Chesson 2000). Enhancing microsite diversity, and thus manipulating niche variety, may allow for a species rich assemblage of plants to colonize, establish, and thrive on green roofs. The findings of Bates and co-workers (2013) support niche theory in a green roof context; the authors reported that on a spatially heterogeneous green roof the substrate texture affinities of forbs and *Sedum* differed and that surface features (e.g. rock piles or woody debris) appeared to serve as moisture refugia for multiple plant species weathering a prolonged drought. Furthermore, Heim and Lundholm (2014) demonstrated that varied substrate depth improved co-existence between a grass and *Sedum* grown on a green roof. However, modification of substrate depth is the only technique aimed at improving plant species richness or survival that has been examined quantitatively on green roofs (Boivin et al. 2001; Bousselot et al. 2011; Dunnett & Nolan 2002; Durhman et al. 2007; Heim & Lundholm 2014; Thuring et al. 2010; VanWoert et al. 2005). The effects of other forms of heterogeneity, such as surface features, remain unknown.

Diversification of green roof plant communities may not only influence green roof functionality; it may also foster greater diversity in the invertebrate communities accessing green roof habitat (Kadas 2006; Madre et al. 2013). Green roofs could offer multiple resources to potential colonizers: food (e.g. pollen, nectar, seeds, plant tissue), water (e.g. via condensation, guttation, or water pooling on irrigated roofs), nest sites and nest building material, and protection from ground-level disturbances. It is clear from multiple sampling surveys that a variety of invertebrates access green roofs (Brenneisen 2006; Braaker et al. 2013; Jones 2002; Kadas, 2006; Rumble & Gange 2013; Madre et al. 2013; Colla et al. 2009; Tonietto et al. 2011; Ksiazek et al. 2012; MacIvor & Lundholm 2011a), and these communities can contain xerophilic specialists and species of conservation concern (Brenneisen 2006; Jones 2002; Kadas 2006; Schrader & Böning 2006). In a survey of multiple green roofs, Madre and co-workers (2013) found more diverse invertebrate communities on roofs with greater plant canopy complexity. Importantly, the few researchers who have compared green roof invertebrate diversity with that of adjacent sites at ground level or sites in non-urban natural locations found that diversity was lower on green roofs (Colla et al. 2009; MacIvor & Lundholm 2011a; Tonietto et al. 2011). Insect richness can be higher in cities relative to adjacent natural areas, though this relationship is taxon- and habitat-specific, and may relate to extent of surface hardening, nutrient availability, and pesticide input (Raupp et al. 2009).

Many researchers who have examined invertebrate communities on green roofs have recommended that increased heterogeneity in the green roof environment would promote greater invertebrate diversity (Jones 2002; Kadas 2006; Brenneisen 2006; Rumble and Gange 2013). If both plant communities and invertebrate communities respond by exhibiting greater diversity, increased environmental heterogeneity may serve to optimize both the ecological and environmental functionality of green roofs. However, surveys of invertebrate communities on green roofs represent only preliminary assessments of green roof habitat value. The presence of an invertebrate on a green roof, particularly an invertebrate with high mobility, does not confirm its usage of specific green roof resources. For example, while bee communities have been documented on several green roofs in North America (Colla et al. 2009; Ksiazek et al. 2014; Tonietto et al. 2011) few have linked these important pollinators to rooftop plant reproduction (Ksiazek et al. 2012) or resource harvesting (MacIvor et al. 2015). Determining whether green roofs serve as high quality habitat requires examination of the survival and community development of green roof plant species assemblages and investigations of the direct usage of green roof resources by their insect visitors.

Thesis Objectives

My research examined the capacity of extensive, native-planted green roofs to serve as habitat for both native plant species (Chapter two) and native bees (Chapter three) in Nova Scotia. Through two experiments, I first assessed the effect of simple green roof modifications, such as the addition of surface features (e.g. pebbles, logs) and the redistribution of soil (to vary surface topography and depth), on native seedling dynamics and soil conditions as measures of habitat value. In the first experiment, surface features and topographic heterogeneity were incorporated into a previously homogeneous extensive green roof in Halifax, Nova Scotia and seeded with a mix of 26 native species. To test the effect of these modifications, I quantified native seedling density and species richness and monitored substrate moisture and temperature over the growing season at 12 potentially distinct microsite types across the roof. I conducted the second experiment on replicated modules simulating green roof growing conditions in a greenhouse environment. In this experiment, I incorporated the same surface features tested on the green roof (i.e. pebble piles, logs) into green roof modules, seeded them with seven native species, and subjected the plants to continuous drought following seedling emergence. To test the effect of the features, I measured seedling density, species richness, soil moisture, and soil temperature before and during the drought. The results of this research will help to determine the effect of environmental heterogeneity on microsite diversity and native plant establishment on extensive green roofs.

In chapter three, my objective was to determine the value of native-planted green roofs as habitat for native bees. I sampled the wild bee communities accessing native-planted green roofs, ground-level urban, and natural coastal barrens sites containing two native plant species, *Sibbaldiopsis tridentata* and *Solidago bicolor*, within Halifax Regional Municipality. To evaluate direct usage of green roof resources, I examined corbicular pollen loads collected by bumblebees (*Bombus spp.*) at these sites to determine the proportional contribution of pollen from plants growing in coastal barrens, in the city, and on the roofs. Habitat provisioning has long been cited as a service provided by green roofs, but this conclusion cannot be supported by species surveys alone. My research projects enhance our knowledge of green roof ecology by quantitatively assessing the capacity of green roofs to provision habitat for both native plants and urban bees.

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Chapter 2

“Native seedling and substrate responses to environmental heterogeneity”

Introduction

In cities, dominance of impervious surfaces and scarcity of green space tend to increase rapidly with proximity to the urban core (Grimm et al. 2008; Tredici 2010). Real estate in the urban core is valuable, leading to a greater allocation of this space for commercial development rather than urban greening. The handful of spontaneously vegetated vacant lots present in a city may harbour significant biodiversity, but are often viewed by residents as 'derelict plots' with little value (Brundtland et al. 1987; Robinson & Lundholm 2012). Several consequences arise from this increase in surface hardening. During significant rain events, large volumes of unfiltered runoff reach stormwater infrastructure in a short period of time, risking overflow events and downstream contamination (Paul & Meyer 2003). Building materials like pavement and conventional roofing absorb much of the incoming solar radiation, increasing heat flux into individual buildings and warming air at the city scale in a phenomenon referred to as the 'urban heat island effect' (Kalnay & Cai 2003). Vehicular exhaust contributes pollutants, such as carbon dioxide, polycyclic aromatic hydrocarbons, nitrogen oxides, and particulate matter, to urban air (Pataki et al. 2006). All of these responses to surface hardening come with financial and environmental costs (Grimm et al. 2008).

Many environmental urban challenges can be mitigated by providing green space in the city: plants trap pollutants, capture and transpire rainwater, reflect incoming solar radiation, and shade underlying surfaces, while soil filters pollutants, retains and delays stormwater, and moderates heat fluxes (Grimm et al. 2008, Oberndorfer et al. 2007). Given the pressures to develop real estate in urban centers, vegetated rooftops, or green roofs, may offer an integrated response to these urban issues without adding to competition for ground-level space. While intensive green roofs require structural adaptation to support their added weight, extensive green roofs, featuring shallow (<20 cm) substrate, represent a less expensive rooftop vegetation alternative that delivers key ecosystem services and protects the underlying roof surface.

The profile of a typical extensive green roof begins with a waterproof membrane base covering the roof deck, followed by a root barrier layer, drainage fabric, growing medium, and a top layer of vegetation. To minimize weight, designers often choose commercial green roof substrate as the growing medium (Oberndorfer at al. 2007). Typical green roof growing media contain little organic matter, between 5-10% of the volume, combined with lightweight mineral components like perlite or expanded shale (Ampim et al. 2010). Shallow substrate depths, limited organic matter content, and the exposed nature of rooftops create challenging growth conditions for green roof plants. Drought constitutes a frequent stress (Oberndorfer et al. 2007). In North America, freezing affects green roof plants in cold climates (Boivin et al. 2001). Heavy rain and high winds can erode growing media, reducing available rooting volume (Appleby-Jones 2014).

The exposed conditions, uniform substrate composition, and shallow depths common among extensive green roofs impose significant constraints, foremost being drought (Dunnett & Nolan 2002), on the variety of plant species considered suitable for inclusion in the vegetation layer. Consequently, succulent plants within the genus *Sedum* have come to dominate commercially installed extensive green roofs (Berghage et al. 2007; Dunnett & Kingsbury 2004; Monterusso et al. 2005; Snodgrass & Snodgrass 2006; VanWoert et al. 2005). Leaf succulence, facultative use of the Crassulacean Acid

Metabolism (CAM) photosynthetic pathway, and a mat-like growth form confer drought and cold tolerance to *Sedum* and are adaptive for survival on green roofs (Köhler 2003). However, the overall outcome of growing *Sedum* can be mixed: succulence and CAM photosynthesis can reduce the stormwater capture efficiency of green roofs primarily vegetated by water-conserving *Sedum* species, while certain species of *Sedum* can cool substrate for neighboring plants, potentially providing relief on hot and sunny days (Berghage et al. 2007; Bousselot et al. 2011; Butler & Orians 2009; Starry et al. 2014).

Similar to the variability displayed by *Sedum,* other plant taxa and life-forms contribute in different ways to the specific ecosystem services generated by green roofs, but early trials testing the survival and growth of native plant species on green roofs demonstrated that, without irrigation, green roof conditions can be too harsh for many native species to persist (Dvorak & Volder 2010; Getter & Rowe 2006; Monterusso et al. 2005). Although not investigated in a green roof context, it is possible that plants able to survive one drought cycle could form a “drought memory” and adjust their future photosynthetic responses to avoid damage or death in water deficit conditions (Walter et al. 2010). Thuring and co-workers (2010) observed reduced growth rates in plants exposed to early drought grown in simulated green roof conditions, though others have demonstrated that growth reductions may be minor and may improve plant survival (Costa et al. 2007). Overall, grasses and forbs demonstrate highly variable responses to green roof environments in both monocultures and mixed plantings (MacIvor & Lundholm 2011; MacIvor et al. 2011; Bousselot et al 2011). Despite this variability, recent work by Lundholm and co-workers (2015) demonstrated that several plant functional traits could be used to reliably predict contributions of plant species to overall green roof ecosystem service provisioning.

These functional traits influence resource use by different plant taxa, with specific traits enabling particular resource use strategies; hence, communities of plants that contain different life-forms likely feature a combination of resource use strategies and distinct adaptations to stressful conditions. Variation in resource use strategies and neighbour interactions underpin the concepts of resource complementarity and facilitation in plant communities. Resource complementarity refers to the distinct resource use patterns exhibited by different plant species: if plants vary in their resource use (e.g. spatially, temporally), overall competition is relaxed for a given resource within that plant community. Facilitation refers to the beneficial interactions that can occur between individual plants within a particular set of environmental conditions, exemplified by the attraction of co-pollinators or provision of shade in hot, water-limited environments (Brooker et al. 2008; Callaway & Walker, 1997).

The concepts of resource complementarity and facilitation have significant implications for green roof plant selection. Individuals growing together in monoculture are likely to contribute to overall green roof performance in a comparable manner, with individual plants similarly excelling at or underperforming for a given function. Mixed plantings, in particular those composed of multiple functional groups or life-forms, have a greater likelihood of demonstrating response diversity in relation to environmental changes, thereby altering the integrated performance of the green roof (Elmqvist et al. 2003).

While monocultures may optimize a single function, such as stormwater capture or thermal regulation, diverse plant assemblages should theoretically optimize a variety of green roof functions simultaneously (Butler et al., 2012; Cook-Patton & Bauerle 2012). This has been observed in certain species assemblages, some of which included plant species from coastal barrens habitat occurring in Nova Scotia (Dunnett et al. 2008; Kolb & Schwarz 1986; Lundholm et al. 2010; MacIvor et al. 2011; MacIvor & Lundholm 2011). Lundholm (2015) found that several species mixtures outperformed the best monocultures at providing specific ecosystem services; furthermore, certain species mixtures optimized multiple ecosystem services better than monocultures when assessed using indices of multi-functionality. Van Mechelen and co-workers (2015) found a positive relationship between species rich green roof plant assemblages and functional diversity.

Beyond functional performance, the higher response diversity of mixed plantings should increase the resilience of green roof vegetation when faced with extreme events, such as prolonged drought or inundation, with functional analogues trading off dominance depending on environmental conditions (Elmqvist et al. 2003). Moreover, in comparison to mixed plantings the high resource concentration represented by monocultures or single-genus plantings may attract dense populations of herbivores and pests (Altieri & Letourneau 1982; Root 1973).

Identifying strategies and designs to create and maintain plant diversity on green roofs is essential, given the potential and observed benefits that derive from diversified green roof plant assemblages. Plant species differ in their affinity for specific growing conditions (Chesson 2000). Consequently, designers that seek to optimize green roof functionality through plant diversity may need to provide a variety of distinct microsites to support planted species through time.

Green roof designers and NGOs in Europe have installed examples of biodiverse roofs, which incorporate greater heterogeneity into the green roof environment. Suggested methods to increase environmental heterogeneity include varying substrate composition and topography, adding surface features, like brush piles or logs, or installing structures that cast shadows, like solar panels (Bates et al. 2013; Brenneisen 2003; Brenneisen 2006; Köhler & Poll 2010; Bousselot et al. 2013). Some roof designs include soil from ground level, collected prior to building construction, or repurposed substrate materials, like crushed brick, which reduce the lifecycle costs of a green roof (Ampim et al. 2010; Brenneisen 2006; Molineux et al. 2009). Guidelines have been produced by the City of Toronto to optimize urban biodiverse roof construction, and guiding documents have been similarly produced by various non-profit organizations (e.g. BugLife, The Green Roof Centre, Living Roofs).

Support for the positive heterogeneity-diversity relationship, upon which these guiding documents are predicated, exists in the ecological literature, but this relationship can be weak at small spatial scales approximating the size of a typical green roof (Lundholm 2009; Stein et al. 2014). Both diversity and cover should be maintained throughout the life of a green roof to ensure optimal multifunctionality; thus, the scale of heterogeneity applied to a green roof in an attempt to promote plant diversity must match that of the plants responding. Seeds represent a method by which plants can disperse to more favourable growing conditions within a green roof. Ksiazek and co-workers (2012) did not observe pollen limitation in plants growing on an irrigated green roof and further demonstrated that forbs grown on green roofs produce high quality seeds comparable to those of ground level conspecifics (2014). During the seedling life stage, plants can be particularly vulnerable to soil moisture deficits and heat stress, common green roof stressors. Seedlings emerging from large seeds tend to establish more readily, but the vulnerability of small-seeded species can be balanced by prolific seed production (Moles & Westoby 2004).

Due to the ability of seeds to disperse across a roof and the sensitivity of seedlings to stressful growth conditions, seedlings are likely to respond positively to the presence of microsites that provide relatively cool and moist substrate on a green roof. Soil conditions indeed exert a strong influence on the vegetation-environment relationship at small (<200 m) scales relevant to green roof research (Siefert et al. 2012). In both controlled greenhouse and harsh glacial foreland environments, seedlings have been observed to respond strongly to heterogeneity provided by, for example, small-scale variation in soil topography or the presence of surface features, including woody debris or rocks (Harper et al. 1965; Jones & del Moral 2005). Both soil moisture and temperature are crucial determinants of seedling recruitment in harsh growth environments (Schwienbacher et al. 2012).

The responsiveness to growth conditions, spatial spread, and size of seedlings make them ideal subjects in the study of small-scale changes to environmental heterogeneity, such as those modifications featured in contemporary biodiverse green roof designs, and their effect on plant diversity. Furthermore, the influence of edaphic conditions on small-scale heterogeneity-diversity relationships suggests that seedlings will respond to treatments that increase microsite substrate moisture and decrease substrate temperature in water limited and thermally variable growth environments characteristic of extensive green roofs. Heterogeneity treatments that successfully produce distinct microsites and favourable growing conditions for seedlings could diversify green roof plant assemblages, provide refuge during periods of heat and water stress, and alleviate irrigation requirements, all while accommodating the shallow substrate depths required for extensive green roof retrofitting.

To date, very little research (Bates et al. 2013) has considered the effect of specific heterogeneity treatments, other than variation in substrate depth (Boivin et al. 2001; Bousselot et al. 2011; Dunnett & Nolan 2002; Durhman et al. 2007; Heim & Lundholm 2014; Thuring et al. 2010; Van Woert et al. 2005), on the substrate conditions and plant dynamics of extensive green roofs, despite the implementation of policies promoting the biodiversity-enhancing potential of biodiverse roofs that incorporate many forms of heterogeneity. No studies have considered the effects of specific heterogeneity treatments on seedling establishment and diversity on green roofs. Through both a green roof field trial and modular greenhouse study, I aimed to quantify the effects of several heterogeneity treatments under ambient green roof conditions and during a prolonged drought on both the creation of microsites with distinct substrate conditions and the response of seedling density and species richness. Plant species included in this study were selected based on prior survival and growth success on Nova Scotia green roofs and/or affinity to analogous natural environments, including coastal barrens, beach, and roadside environments (MacIvor & Lundholm 2011; Lundholm et al. 2010). I hypothesized that logs, pebble piles, and deep substrate would create wetter and cooler microsites, and that these locations would host a higher density and more species rich assemblage of seedlings. I further hypothesized that rates of soil moisture loss would be attenuated in locations with pebbles and logs during a prolonged drought, and that this would result in greater seedling density and species richness at these sites with surface features compared to featureless controls.

Methods

Green roof experiment

Site

Measurements of seedling dynamics and soil conditions were collected June-September 2014 across an extensive green roof on Saint Mary's University campus in Halifax, NS (Figure 1). The green roof was installed on the fifth story of the Atrium building in 2010 and features an east-west oriented 24 m x 9 m vegetated rectangular footprint. At the time of installation, a homogeneous depth of 7.5 cm of commercial green roof growing medium (Soprema Inc., Drummondville, QC) was applied on top of extensive green roof drainage containers (ELT EasyGreen, Brantford, Ontario) positioned over the roof membrane, below which a 2.5 cm plywood protection board abuts insulation (5–15 cm of rigid polyisocyanurate, R = 5 per 2.5 cm) sitting above the steel roof deck. Using rubber pond liner and metal edging, the roof was partitioned into eight sections (plots), measuring 6 m x 4.5 m, each with a dedicated drain; each of these eight plots was subdivided into six subsections (subplots) approximately 2 m × 4.5 m, which share substrate water ($n = 48$ subplots). The green roof receives partial shade from buildings on its west and south. It has not received supplemental irrigation or fertilizer.

Following installation in 2010, each subplot of the green roof was plug planted at 15 cm intervals with native coastal barrens plant species. The species included *Danthonia* *spicata*, *Sibbaldiopsis tridentata*, and *Solidago bicolor*. Bare substrate separating these original plantings has been unevenly colonized by these same species, along with lichens and several species of moss, a mix of weedy cosmopolitan forbs (e.g. *Epilobium ciliatum, Cerastium sp., Conyza canadensis, Plantago major, Taraxacum officinale, and Senecio viscosus*), and a small number of species whose propagules likely originated from adjacent green roof modules, including *Anaphalis margaritacea, Sedum acre, Campanula rotundifolia, Symphyotrichum novi-belgii,* and *Festuca rubra.* The roof has been maintained with periodic weed removal since 2010.

For this experiment, the green roof was modified to include greater environmental heterogeneity and seeded with a mixture of native plants. In November 2013, several surface features and depth modifications were randomly assigned to and incorporated into each of 48 subplots on the green roof. All experimental subplots were seeded with a mix of 26 plant species (Table 1), standardized by weight. Seeds and berries were collected locally from coastal barrens, beach, marsh, and roadside environments within the Halifax Regional Municipality from September - November 2013, with the exception of *Aquilegia canadensis*, which was purchased as seed. Seeds were cleaned and stored at 4°C prior to application on the green roof.

The original green roof design, which featured a single substrate type and depth (7.5 cm) across the entire vegetated area, was modified to increase overall green roof environmental heterogeneity. Surface features (logs and pebble piles), variation in substrate topography and depth (substrate redistribution), and a combination of surface features and variability in substrate topography were all incorporated into the roof. The locations of each these modifications were randomized across the roof to account for variation in solar exposure, mature vegetation cover, and other uncontrolled environmental factors. Some areas of the roof were not modified from the original design (7.5 cm mean substrate depth) so that unmodified conditions (homogeneous microsites) could be compared to those that received features, underwent depth modification, or both. Pebble piles (~20 cm diameter, ~5 cm high) were composed of white landscaping pebbles (Kent Building Supplies, Dartmouth, NS) placed directly on the substrate surface (7.5 cm mean substrate depth). Logs were sourced from local yard waste following pruning of Norway maple (*Acer platanoides*) branches (~20-25 cm length, ~5 cm diameter, bark present); logs were placed directly on the substrate surface (7.5 cm mean substrate depth). To create areas with varied substrate depth and topography, substrate was redistributed to create regions of substrate 2-3 cm deep and regions of substrate 10-12 cm deep. Finally, some areas of the roof received surface features (logs and pebble piles) that were placed directly on the substrate surface over both shallow (2-3 cm) and deep (10-12) substrate; this allowed for an investigation of the interactive effects of substrate depth and surface features on variables of interest.

Pre-weighed mixtures of cleaned seeds and whole berries were hand broadcast onto each individual subplot in December 2013 to ensure seeds would be exposed to natural overwintering conditions. Additional seed from all 26 species was retained and stratified at 4°C for three months (December 2013 – March 2014). Germination trials were conducted for all species March – June 2014; 20 seeds per species were placed on wetted filter paper in sealed petri dishes (*n* = 3, for 26 species) located under growth lights set for a 12-hour photoperiod. Emerging seedlings were photographed and a seedling image library was developed to facilitate seedling identification over the growing season.

In May 2014, permanent 10 cm x 10 cm quadrats were added to the green roof, which constituted the experimental sampling units. These quadrats were established across the green roof in locations predicted to display distinct substrate conditions (e.g. cooler temperatures, increased substrate moisture) at potentially unique microsites (e.g. log edge, pebble center, deep substrate with log) created by the green roof modifications. This fully factorial (3 x 4) design included three different depths (shallow (2-3 cm), control (7.5 cm, original depth of unmodified roof), and deep (10-12 cm)) and four substrate surface conditions (bare, log, pebble centre, pebble edge), constituting 12 potentially unique microsite types (*n* = 8 for each microsite type; Figure 2). The location of each quadrat was assigned randomly.

Data collection

Soil moisture content and afternoon soil temperature were quantified in all quadrats to determine whether the 12 microsite types affected the growing conditions experienced by seedlings emerging on the green roof. Following a 25 mm rain event on June 14 and a 9 mm rain event on June 15, 2014 (Environment Canada, Shearwater RCS, NS), soil moisture content (%) of green roof substrate was measured once daily in each quadrat using a handheld GS3 Ruggedized Soil Moisture, Temperature, & Electrical Conductivity Sensor (Hoskin Scientific Limited, Burlington, ON) and ProCheck data logger (Decagon Devices, Inc., Pullman, WA, USA) from June 15 to June 17, 2014. No precipitation occurred during the substrate moisture measurement period. This rain event was significant but not extreme, and was meant to represent a typical precipitation event and subsequent dry down conditions on a green roof in Halifax. Data were averaged over the three days to calculate mean substrate moisture content. Afternoon substrate temperature (°C) was measured in all quadrats on July 20 (maximum air temperature 23°C; Environment Canada, Shearwater RCS, NS) and July 22 (maximum air temperature 24°C; Environment Canada, Shearwater RCS, NS), 2014, as these represent typical warm summer days in Halifax. Substrate temperature was collected by inserting a 9878E Pocket Digital Thermometer (Taylor Precision Products, Inc., Oakbrook, Illinois) down to the substrate base. Measurement order was reversed between sampling days as air temperature increased steadily over the 2-hour sampling period. Afternoon substrate temperature data were averaged over the two days sampled to calculate mean substrate temperature.

Both substrate temperature and moisture content are influenced by incident solar radiation. Substrate on the green roof is shaded unevenly by surrounding buildings. To account for this disparity, solar exposure was assessed for each quadrat. The coordinates of each quadrat on the roof were determined using a tape measure. A georeferenced map of the Atrium green roof was generated in ArcGIS (ArcGIS 10.2.2, Environmental Research Systems Institute, Redlands, California) and was combined with the spatial coordinates for the quadrats, according to Buckland-Nicks (2015). Using this map, incident solar radiation values (KWh/m^2) were modelled for each quadrat for the growing season (May-September).

Seedling density (total count of seedlings in 100 cm^2) and species richness (total count of species in 100 cm^2) were measured in all quadrats to determine whether microsite type affected the number and diversity of seedlings persisting on the green roof.

Seedlings were counted and identified to species by the same observer monthly from June to September 2014. The roof was not weeded during this time. Mature vegetation can affect seedling emergence and survival; due to an uneven distribution in pre-established vegetative cover across the green roof, overhead photographs (standard camera height of 3 m) were taken of all subplots in May 2014 prior to seedling emergence. Percent vascular plant cover for each subplot was determined within each photo via point counting (minimum 350 points assessed per photo within a recursive grid) using JMicroVision v1.2.7 (Roduit 2014).

Data Analysis

Separate two-way (3 x 4) factorial analyses of covariance were implemented to assess whether mean (average of values from June 15-17) substrate moisture content ($F_{13, 82} = 10.8$, $p = 5.3E\text{-}13$; adjusted $R^2 = 0.86$) and mean (average of values from July 20 and 22) substrate temperature ($F_{13, 82} = 46.6$, $p < 2.2E\text{-}16$; adjusted $R^2 = 0.57$) were affected by two factors, the depth of substrate (3 levels: shallow (2-3 cm), control (7.5 cm), and deep (10-12 cm)) and the presence of surface features (4 levels: none, log, pebble edge, pebble centre), or their interaction ($n = 8$, for each of 12 depth-feature pairs). Two continuous covariates were included in the ANCOVA, modelled total solar radiation (KWh/m^2) and pre-established vascular plant cover (%). Independence of predictors and covariates was tested and confirmed; homogeneity of regression slopes was confirmed for substrate temperature but not for substrate moisture (interaction between total solar radiation and surface feature, $p = 0.036$). The covariates were not significantly correlated ($R^2 = 0.08$).

Due to data overdispersion ($\theta = 2, 1.7$, for June and September seedling density data, respectively) and non-normality, a negative binomial generalized linear model (link function = ln) was fitted to determine how seedling density at each microsite type compared to the seeded control sites (separate models for June and September). Microsite was included as a factor with 12 levels and was dummy coded to set the seeded control microsite type as the intercept. Total solar radiation was centered, as no ‘true’ zero existed in the data, and was included as a factor. Regression coefficients were exponentiated to generate incident rate ratios (IRRs) on the scale of the response variable (seedling density). Using the sandwich package in R (Zeileis 2004), robust standard errors were calculated and used to generate the 95% confidence intervals of the IRRs for each factor level, as suggested for count data (Hilbe 2014). The negative binomial GLM was fitted using the MASS package in R (Venables & Ripley 2002).

Due to data non-normality and Poisson variance structure, a Poisson generalized linear model (link function = ln) was fitted to determine how species richness at each microsite type compared to the seeded control sites, again with centered total solar radiation included as a factor (separate models for June and September). Microsite was included as a factor with 12 levels and was dummy coded to set the seeded control microsite type as the intercept. IRRs and 95% confidence intervals were generated as with the negative binomial GLMs. Poisson GLMs were fitted using the stats package in R (R Core Team, 2014). Only those species that successfully germinated in at least one green roof quadrat, and which had been applied in the original 26 species seed mix, were included in the analysis. *Danthonia spicata*, *Sibbaldiopsis tridentata,* and *Solidago bicolor* were excluded, as seedlings of these species recruited in 2014 may have originated from propagules produced by adult conspecifics growing on the green roof.

All grasses were also excluded, as most seedlings died before a definitive identification could be completed.

Permutational multivariate analysis of variance (PERMANOVA) was used to test for differences in June seedling community composition among microsite types. Datasets from other months were not tested due to high seedling mortality over the summer. Species inclusion criteria were identical to those used when specifying the Poisson GLMs. The PERMANOVA function was executed via the vegan package in R (Oksanen et al. 2007). To assess seedling species inventory completeness and total species richness in heterogeneous and homogeneous green roof environments, sample-based and individual-based rarefied species richness curves (n = 96 quadrats, for 11 microsite types included in heterogeneous treatment (i.e. all microsite types with controls excluded); n = 24 quadrats, for 1 microsite type (seeded control) included in homogeneous treatment) were generated (100 runs without replacement) using EstimateS 9.1.0 (Colwell 2005) and plotted using ggplot2.

Greenhouse experiment

Site

Monitoring of substrate conditions and seedling dynamics in replicated modules simulating a green roof growth environment was conducted in the greenhouse facilities on the Saint Mary's University campus in Halifax, Nova Scotia (Figure 3). Square plastic trays with free-draining bases, measuring 36 cm x 36 cm, constituted the experimental sampling units. These modules were lined with a composite non-woven water retention layer (Huesker Inc., Charlotte, NC, USA), an Enkamat drainage layer, and a filter layer

(Colbond Inc., Enka, NC, USA). Substrate consisted of Sopraflor X (Soprema Inc., Drummondville, QC), and modules were uniformly filled to 2 cm below the top of the tray lip to provide a substrate depth of approximately 7 cm.

In this study, a subset of the modifications incorporated into the Atrium green roof were applied to the experimental modules and seeded with a mixture of seeds of seven native plant species: *Anaphalis margaritacea*, *Plantago maritima*, *Solidago bicolor* (forbs); *Sibbaldiopsis tridentata, Vaccinium macrocarpon* (shrubs); *Danthonia spicata* (grass), and *Rhodiola rosea* (succulent). Seeds and berries were collected locally from coastal barrens and roadside environments within the Halifax Regional Municipality from September - November 2014. Seeds were cleaned of debris and stored at 4°C prior to application to the modules. *Anaphalis margaritacea* and *Danthonia spicata* were stored dry; all other seeds were stored on moistened paper towel. Seeds contained within berries were manually removed from the berries.

Both surface features (logs and pebble piles) were applied to the modules and paired with bare substrate, seeded controls. Modules assigned to the "log" treatment (*n* = 12) were modified to include a single section of wood from Norway maple (*Acer platanoides*) branches (~20-25 cm length, ~5 cm diameter, bark present) placed in the center of the module, directly on the substrate surface (Figure 3). Modules assigned to the "pebble" treatment (*n* = 12) were modified to include a single centrally located rectangular pile (height ~5 cm, width ~12-15 cm, length 36 cm) of white landscaping pebbles (Figure 3). Control modules (*n* = 12) only received the seven-species seed mix.

To ensure that both the density and location of seeds were identical in each module (*n* = 63 seeds, for each of 7 plant species), 36 cm x 36 cm grids were used to guide individual seed placement (Figure 4). The grids featured 21 guidelines spaced 1 cm apart, with 21 points per line at 1 cm spacing. A buffer of 7.5 cm was left surrounding the outside of the grid on all edges to avoid seed placement near the inner edges of the module, thus reducing edge effects. Each species to be seeded was randomly assigned three of the 21 guidelines per module for a total of 63 seeds per species placed on each module surface (443 total seeds per module). Lines of seeds were oriented perpendicular to surface features, so that species would be evenly spread across the module substrate and surface feature. This seed application format prevented clumping of seeds and ensured that each species encountered the range of conditions presented by each heterogeneity treatment. Seed placement occurred from February 6-13, 2015. Modules were watered to field capacity on February 13, once all seeds had been placed. Modules were watered to field capacity every other day from February 13, 2015 to June 11, 2015 to facilitate germination and establishment of plants. Modules were watered to field capacity on June 11, 2015 after which all watering was terminated. Module locations were randomized, and modules were reassigned new random locations every third week to minimize the effects of spatial variability in the greenhouse environment.

Data collection

Substrate moisture content and afternoon substrate temperature were quantified in all modules to determine whether logs and pebble piles affected substrate conditions during an extended drought. Measurements of substrate moisture content (%), substrate temperature (°C), seedling density, and species richness were collected weekly, beginning June 11, 2015 and ending July 23, 2015.

Soil moisture content was measured using a handheld GS3 Ruggedized Soil Moisture, Temperature, & Electrical Conductivity Sensor (Hoskin Scientific Limited, Burlington, ON) and ProCheck data logger (Decagon Devices, Inc., Pullman, WA, USA). The sensor was inserted down to the substrate base, either at the edge of a surface feature, in log or pebble treated modules, or centrally, in control modules. Substrate temperature was collected by inserting a 9878E Pocket Digital Thermometer (Taylor Precision Products, Inc., Oakbrook, IL, USA) down to the substrate base, with thermometer placement in relation to surface features matching that of the soil moisture sensor.

Seedling density (total count of seedlings in each module) and species richness (total count of species in each module) were measured to determine whether logs or pebble piles affected the number and diversity of seedlings persisting in the experimental green roof modules. Seedlings were counted and identified to species by the same two observers, and weeds were removed when found. Plants were considered dead when they no longer displayed green leaf or stem tissue.

Data Analysis

Due to data overdispersion in initial species abundance ($\theta = 25.8$) and non-normality of residuals, a negative binomial generalized linear model (link function = ln) was fitted to determine how initial abundance compared among species with species included as a 7-level factor; analysis of deviance was used to assess significance ($\alpha = 0.05$) of the main effect of species, from the car package in R (Fox et al. 2009). 95% confidence intervals of initial abundance were generated using the ggplot2 package in R (Wickham 2009). Weekly means were calculated for substrate moisture content, substrate temperature, seedling density, and species richness from drought week 0 (June

11, 2015) to drought week 6 (July 23, 2015) for each treatment. Significant differences among treatments were assessed by calculating and plotting the 95% confidence intervals for each response variable against time (drought week). Confidence intervals were calculated and displayed in R using the ggplot2 package.

Results

Green roof experiment

Growing conditions

Incident solar radiation varied considerably across the green roof; the most shaded roof location received 400 KWh/m^2 less radiation than did the sunniest, which received 730 KWh/m^2 (Figure 5). Likewise, cover of pre-established vascular plants ranged from 0.6% to 50% of the area contained in a subplot, with intervening substrate surfaces covered primarily by mosses or, less frequently, lichens. Remaining surface area on the green roof was characterized by exposed substrate.

Substrate temperature

Total solar radiation and vegetation cover both significantly affected mean substrate temperature (± SE) on the Atrium green roof, and substrate depth and surface feature type displayed a significant interaction (Table 2). Each 100 KWh/m^2 increase in solar radiation warmed green roof substrate by approximately 1.7°C (± 0.3°C) while each 10% increase in vegetation cover cooled green roof substrate by approximately 0.5°C (± 0.2°C). When uncontrolled variation in solar radiation and vegetation cover were taken into account, several of the microsite types tested in this experiment altered the growing conditions of the green roof by affecting both substrate temperature and substrate moisture content (Table 2, Figure 6). The hottest microsites on the green roof (41.5 ± 0.7°C) had shallow substrate and no surface features; the coolest microsites all occurred over deep substrate and were located at the center of pebble piles (26.6 ± 0.5) and at the edge of logs (26.5 ± 0.9) (Table 3).

Substrate depth significantly affected temperature at the substrate base (Table 3); locations on the green roof that featured deep (10-12 cm) substrate were cooler (29.2 ± 1.1°C) and those that featured shallow (2-3 cm) substrate were hotter (41.5 ± 0.7°C) than locations at which substrate depth (7.5 cm) was not modified (35.9 ± 2.0°C) (Table 3, Figure 6). This represents a difference of greater than 10°C between deep and shallow green roof substrate on a hot summer day.

Surface features appeared to cool substrate, but their effect on temperature was weaker than that of depth (Table 3; Figure 6). Furthermore, the cooling effect of any given surface feature was reduced as substrate depth increased (Figure 6). At microsites with deep substrate, the presence of any surface feature effected a maximum temperature reduction of 2.7°C (Table 3, Figure 6). However, at shallow substrate locations, surface features reduced temperatures by 5.2-7.8°C (Table 3, Figure 6).

Substrate moisture

In addition to substrate temperature, substrate moisture (mean ± SE) content was significantly affected by total solar radiation, vegetation cover, substrate depth, and surface features (Table 2, Figure 6). Each 100 KWh/m^2 increase in solar radiation decreased green roof substrate moisture by approximately 1.4% (± 0.5%) while each 10% increase in vegetation cover resulted in a 0.5% (± 0.2%) increase in substrate water content. When uncontrolled variation in solar radiation and vegetation cover were taken into account, increased depth and the presence of some surface features decreased green roof substrate moisture content compared to unmodified microsites (Table 2, Figure 6). Locations with deep substrate at the center of pebble piles represented the driest locations on the green roof and exhibited an average soil moisture content 10.8% lower than control locations; no microsite types were significantly wetter than locations with unmodified substrate depths (7.5 cm) that lacked surface features (Table 3).

Though microsites with deep and shallow substrate featured similar moisture contents (32.2 ± 0.7%, 33.3 ± 1.6%, respectively), both displayed lower moisture contents than locations with unmodified depth (37.7 ± 0.6%). At microsites with both unmodified and deep substrate, drier conditions were observed for substrate under pebble piles relative to bare substrate at the same depth (Figure 6), with moisture reductions ranging from 7.1-3.3% (Table 3). However, logs and the edges of pebble piles increased the moisture content of shallow substrate by 2.3% and 3.2%, respectively (Table 3).

Seedling Dynamics

Although a mix of 26 native plant species was broadcast onto the green roof, only nine species were observed in quadrats (with *S. tridentata, S. bicolor,* and all grasses excluded): *A. margaritaceae, A. canadensis, Atriplex spp., C. edentula, C. sepium, C. rotundifolia, O. biennis, P. maritima,* and *R. rosea*. In laboratory germination trials, at least one seed germinated in 22 of the 26 species tested, and 12 species achieved germination rates above 50% (Table 4). Although many plant species failed to germinate in the monitored quadrats, a few species were observed to be growing outside of the quadrats including *L. japonicus*, *P. trifoliolata*, *S. novi-belgii*, and *S. sempervirens*. Of those seedlings found to have successfully germinated on the green roof (outside of the monitored quadrats), two species, *M. pensylvanica* and *P. trifoliolata*, had failed to germinate under laboratory conditions; conversely, while six of the nine shrubs germinated successfully (four of which achieved germination rates in excess of 60%, including one species (*V. macrocarpon*) which experienced a germination rate of 100%) in the laboratory trial, only two shrub species were found on the green roof.

Seedling Density

Averaged across all quadrats, seedling density was low in both June (3.2 ± 0.4) and September (2.7 ± 0.3). Although many different types of microsites affected the abiotic growth conditions present on the green roof, fewer microsite types impacted seedling density significantly in June and September (Table 5; Figure 7). In both months, the greatest increase in seedling density was observed in microsites with deep substrate and no surface features, with seedling density increased by a factor of 6.0 (± 1.4) in June and a factor of 5.8 (± 1.6) in September, relative to unmodified microsites. Locations with both deep substrate and logs also exhibited significantly higher seedling densities compared to unmodified microsites, with 3.8 (± 1.5) times greater seedling density in June and 5.2 (± 1.7) times greater seedling density in September. Microsites with shallow substrate located at the edge of pebble piles were the only other microsites to display higher seedling densities than controls in both June and September, with seedling density increased by a factor of 2.8 (± 1.5) in June and 3.6 (± 1.5) in September. Three further microsites significantly increased seedling densities in September but not in June; microsites in deep substrate located at both the edge and the center of pebble piles increased seedling density by a factor of 3.6 (± 2.1, 1.7, respectively), and microsites at the edge of pebble piles over unmodified substrate increased seedling density by a factor of 3.1 (± 1.6) compared to unmodified microsites.

Species Richness

Averaged across all sites, species richness only reached 1.3 (± 0.1 species) per quadrat in June and September. Only two microsite types on the green roof significantly affected species richness, increasing species richness in both June and September (Table 6, Figure 8). Microsites with deep substrate and no surface features increased seedling species richness by a factor of 3.1 (± 1.2) in June and September. Species richness was additionally increased at microsites with both deep substrate and logs, increasing 2.9 times (± 1.2) that of controls in June and September.

Community composition

Results of a PERMANOVA indicated that microsite type did not significantly alter which seedling species grew together at different microsites on the green roof. When all unique microsites were combined and compared to seeded controls only, both sample-based and individual-based rarefied species richness curves indicated that the total number of species occurring in the heterogeneous environment did not differ from that sampled in the homogeneous green roof environment, though the community inhabiting control sites appeared to level off at seven species (Figure 9).

Greenhouse experiment

All seven plant species successfully germinated in the greenhouse trial, though initial abundances varied significantly among species ($p < 2.2e-16$) (Figure 10). *A. margaritacea* (13 ± 7) and *D. spicata* (5.8 ± 3.1) established significantly lower initial abundances than all other species. *R. rosea*, *S. tridentata*, and *S. bicolor* achieved similar initial abundances (22.9 ± 9, 27.2 ± 5.6, 20.3 ± 7, respectively), all of which were significantly lower than those observed for both *P. maritima* (42 ±6.0) and *V. macrocarpon* (41.4 ±7.0). Both *V. macrocarpon* and *S. tridentata* demonstrated greater initial abundances in control modules (47.8 ± 6.3, 31.7 ± 5.1, respectively) compared to log (37.8 ± 5, 26 ± 3.5) and pebble (38.7 ± 4.9, 23.8 ± 4.9) treatments.

Substrate Conditions

Substrate conditions in control, log, and pebble treated modules were similar from drought day 0 through two weeks of drought (Figure 11). Modules with pebble piles experienced significantly cooler substrate conditions from the third to the sixth week of drought and significantly wetter substrate conditions from the third to the fifth week of drought (Figure 11). Though significant, these differences in temperature were small, with temperature reductions ranging from 2.2°C at week 4 and 0.7°C at week 6 of drought. Similarly, modest increases in substrate moisture content of pebble treated modules ranged from 2.8% during week 3 to 0.9% at week five relative to controls. By week 5 of drought, the mean substrate moisture across all treatments was very low (0.9 ± 0.1%), and differences in substrate moisture were no longer significant among treatments after six weeks of drought. Substrate conditions in modules with logs did not appear to differ significantly from control or pebble treatments.

Plant Dynamics

In this study, plant density appeared to decrease rapidly when substrate moisture content fell below 10% (Figure 12). From drought day 0 through the first two weeks of drought, plant density in control modules was significantly greater than that of modules with pebble piles (Figure 11). The difference in plant density between control and pebble treated modules ranged from 28.3 plants on drought day 0 to 23.3 plants during drought week 2. During drought week 3, plant densities did not differ significantly among treatments. By drought week 4, pebble treated modules displayed significantly higher seedling density (122.3 ± 6.2) than controls (89.9 ± 5.9). Although pebble treated modules displayed the greatest seedling density among treatments in drought weeks 5-6, the trend was no longer significant.

All seven species survived in all three treatments from drought day 0 though the first week of drought (Figure 11). By drought week 3, species richness was significantly higher in pebble treated modules (6.9 ± 0.08) relative to controls (6.25 ± 0.1). Similar to seedling density, this trend was maintained until the end of the experiment at drought week 6, but was no longer significant.

Discussion

Substrate Conditions

On the green roof, both substrate depth and surface features affected temperature at substrate base, indicating that the heterogeneity treatments did create distinct thermal conditions. As predicted, increased depth and surface features cooled substrate, with their combination effecting the largest temperature reduction. Surprisingly, these reductions were larger than those predicted for the entire gradient of shade across this green roof; the most shaded location on the green roof received 400 KWh/m^2 less solar radiation than the sunniest, which was predicted to produce a maximum temperature reduction of 6.8°C. In comparison, microsites with 10-12 cm substrate located at the center of a pebble pile or next to a long were 9.3-9.4°C cooler than controls, with a 14.6°C difference between the hottest (2-3 cm substrate) and coolest (10-12 cm substrate beside log) microsite type. Despite similar overall mean substrate temperatures (32°C green roof, 28°C greenhouse) surface features placed over 7.5 cm substrate reduced temperatures by 6.4°C on the green roof, while modules located in the greenhouse with 7 cm substrate experienced a more modest cooling effect, achieving a maximum temperature reduction under pebble piles of 2.2°C. Indirect solar exposure in the greenhouse may have contributed to this effect reduction, which indicates that these features would produce the strongest effect on roofs which receive little shade from surrounding buildings. Indeed, with a maximum substrate temperature of 41.1°C, seedlings adapted to Halifax's cool, maritime climate may be approaching their thermal limits, and any cooling effect would reduce stress on vulnerable seedlings.

Unlike their effect on temperature, the influence of microsite type on substrate moisture content did not manifest as predicted. Locations with both shallow and deep substrate experienced drier conditions relative to controls. These patterns may be explained by the topography of plots assigned to the depth heterogeneity treatment. Shallow microsites were located in depressions between hillocks of deep substrate, which represented topographic maxima on the green roof. Rainwater on the roof likely collected in these localized catchment basins and the small volume of substrate present would have been more readily saturated than areas with deep substrate. In this study, substrate moisture content was averaged over three days immediately following a rain event. While shallow microsites would display higher initial moisture content relative to locations with deep substrate immediately after a rain event, they would also lose water at a more rapid rate; this pattern would produce similar 3-day mean substrate moisture values for deep and shallow microsites. In a system with flat topography (i.e. vertical profile held constant), Heim and Lundholm (2014) found that deep substrate was cooler and stored more water than shallow substrate, further suggesting that the hillocky topography in this study influenced microsite moisture conditions.

Another surprising trend indicated that pebble piles on the green roof produced drier substrate conditions than sites without surface features. Dry areas under pebble piles on the green roof could have resulted from an enhancement of runoff caused by reduced permeability of the pebble surfaces relative to substrate. The pebble piles were dense and slightly mounded, which may have directed runoff away from substrate directly below the pile. While soil moisture was not measured during relatively dry conditions on the green roof, it was monitored in the greenhouse over six weeks of sustained drought. Results from the greenhouse study indicate that when initial moisture levels (representing well-watered conditions) are comparable between control and pebble pile treated green roof modules, rates of water loss are reduced under pebble piles during drought. Thus, while microsites under pebble piles may not represent the wettest conditions on a green roof soon after a rain event, they may play a more important role by slowing water loss during drought and reducing overall moisture variability.

It is significant that distinct environmental microsites can be produced in a green roof system with only minor modifications to substrate depth (addition of 3-5 cm of growing medium) and through the inclusion small surface features. Depending on the arrangement of surrounding buildings, incident solar radiation can vary considerably across a green roof, as was demonstrated in this study. Plants growing near to or within a surface feature benefit from decreased temperatures and reduced rates of water loss within the substrate, similar to the effect of shade. However, the small size of the surface features in this experiment would have allowed plants to capitalize on both moderated soil conditions and high light levels. Work by Buckland-Nicks (2015) indicated that on the same roof monitored in this study, high plant mortality occurred in shallow, hot, and dry locations of the roof. Thus, by creating microsites with both surface features and deep substrate, which lose water more slowly than bare soil, sun-loving plants may be able to better establish in low-shade areas of the roof. Additionally, particularly shady regions of a green roof may improve establishment of shade-adapted plant species, which are prone to photoinhibition and photodamage at high light intensities (Chapin et al. 1998).

Seedling Dynamics

Despite strong effects on substrate conditions, fewer microsite types affected seedling density. The green roof represented a challenging growth environment for the seedlings, made evident by low germination rates across the roof, compared to results from a laboratory germination trial, and few germinating species. Nevertheless, deep substrate, with or without surface features, promoted greater seedling densities relative to controls on the green roof, and pebble piles over 7 cm substrate slowed mortality of seedlings during drought in the greenhouse. Bates and co-workers (2013) observed that surface features appeared to act as moisture refugia for plants on a biodiverse roof, though this effect was not quantified or tested statistically. Plant survival is often observed to increase with substrate depth on green roofs (Boivin et al. 2001; Bousselot et al. 2011; Dunnett & Nolan 2002; Durhman et al. 2007; Thuring et al. 2010; Van Woert et al. 2005), which is attributable to greater substrate moisture (Dunnett & Nolan 2002) and, in northern locations, reduced winter injury (Boivin et al. 2001). In this study, shallow microsites located near pebble piles also displayed greater seedling density relative to controls, indicating that these features may make ultrathin (2-3 cm substrate) green roofs more hospitable to plants. However, results from this study only captured the effect of these heterogeneity treatments during a single growing season. Overwintering injury may still limit plant growth in shallow locations, whether or not pebbles are present.

Few microsite types increased seedling species richness relative to control sites. Locations on the green roof that had deep substrate, with or without logs, exhibited greater species richness than controls. Because of low germination on the green roof, seedling communities that developed were species poor and the microsites sampled did not generate distinct seedling communities. It is possible that with greater sampling differences would have been detected between heterogeneous and homogeneous green roof environments, as seeded controls quickly achieved maximal species richness with only seven seedling species, whereas the slope of the rarefied species richness curve indicates that seedling communities in the heterogeneous environment contained undocumented richness. However, at the sampling intensity achieved in this study, total richness of these two communities could not be differentiated.

In the greenhouse, modules with pebble piles delayed the loss of species during drought. Notably, no treatments reduced species richness or accelerated species loss. Initially species rich plantings have been observed to become less species rich over time (Lundholm et al. 2014); thus, inclusion of these microsite types may moderate species loss on green roofs while also increasing survivorship in hot, dry sites on green roofs. In the harsh environment of a glacier foreland, seedling affinities for particular microsite characteristics were shown to diminish in later stages of succession (Jones & del Moral

2005). Consequently, seedling responses to the microsite conditions created by these heterogeneity treatments may vary with green roof age.

Native plants often exhibit high mortality rates on non-irrigated green roofs, with seedlings exhibiting even greater sensitivity to water and heat stress; thus, heterogeneity treatments appear to offer a simple method to facilitate establishment of native species seeded onto low maintenance extensive green roofs. A high degree of self-sustainability is important for any given green roof plant assemblage to minimize maintenance costs over the life of the roof. Although seedling communities studied here were species poor, results from rarefied species richness curves suggest that communities on heterogeneous green roofs may harbour richer plant communities than homogeneous counterparts; however, further work is needed to determine this with certainty. In a review of the literature on the biodiversity conservation potential of green roofs, Williams and co-workers (2014) found scant support for claims that green roofs promote biodiversity. Results from this study indicate that while green roof professionals should be cautious when making claims about the biodiversity benefits of particular green roof designs that remain scientifically untested, some relatively minor modifications can improve seedling germination and survival under challenging growth conditions. More importantly, policymakers should not treat the creation of biodiverse rooftops and ground-level restoration efforts as equally valuable contributions to urban biodiversity when the conservation value of these features has not been adequately quantified.

Conclusion

Plant mixtures show great potential to optimize many of the functions that attract investment in green roofs from developers. Some native and non-native plant species appear to perform as well as or better than commercially available succulents, but widespread inclusion of these plants in extensive green roof plantings has been stymied by repeated observations of low survival and growth. While such limitations can be overcome with increased maintenance and irrigation, these management regimes increase the lifetime cost of green roofs. Finding alternative, low-effort methods of supporting mixed plantings and ensuring their long-term viability is therefore fundamental to increasing the acceptance and success of mixed species planting designs for extensive green roofs. The results of both the green roof and greenhouse experiments included in this study indicate that minor modifications to green roof designs can improve seedling survival and reduce species loss during periods of heat and water stress. Future research efforts must explore the long-term impacts of surface features and substrate topography on the development of green roof plant communities, and should examine the effects of these treatments in different climates and during winter conditions.

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Tables

Table 1. List of 26 native plant species seeded onto the Atrium green roof in December 2013; starred (*) species were collected from local coastal barrens habitat.

Forbs	**Shrubs**	**Grasses**	**Succulents**
Anaphalis margaritaceae	_Arctostaphylos uva-ursi*_	_Calamagrostis pickeringii*_	_Cakile edentula_
Aquilegia canadensis	_Empetrum nigrum*_	_Danthonia spicata*_	_Rhodiola rosea*_
Atriplex spp.	_Empetrum eamsii*_	_Deschampsia flexuosa*_	
Calystegia sepium	_Gaultheria procumbens*_		
Campanula rotundifolia	_Juniperus communis*_		
Lathyrus maritima*	_Morella pensylvanica*_		
Limonium carolinianum	_Sibbaldiopsis tridentata*_		
Oenothera biennis	_Vaccinium angustifolium*_		
Prenanthes trifoliolata	_Vaccinium macrocarpon*_		
Plantago maritima*			
Solidago sempervirens*			
Symphyotrichum novi-belgii			

Table 2. P-values from separate two-way analyses of covariance modeling the effect of total solar radiation (KWh/m^2, covariate), vegetative cover (%, covariate), and the interaction of substrate depth (3 level factor: shallow (2-3 cm), control (7.5 cm), and deep (10-12 cm)) and feature type (4 level factor: bare, log, pebble edge, and pebble centre) on Atrium green roof afternoon substrate temperature ($F_{13, 82} = 10.8$, p = 5.3E-13; adjusted $R^2 = 0.86$) and substrate moisture content ($F_{13, 82} = 46.6$, p < 2.2E-16; adjusted $R^2 = 0.57$).

Response	Predictor	SS	DF	F-value	P-value	
Temperature	Solar radiation	134	1	40.0	1.3E-08	*
	Vegetation	34	1	10.3	1.9E-03	*
	Depth	1221	2	182.7	2.2E-16	*
	Feature	414	3	41.4	2.2E-16	*
	Depth x Feature	63	6	3.1	8.4E-03	*
	Residuals	*274*	*82*			
Moisture	Solar radiation	94	1	9.9	0.002	*
	Vegetation	43	1	4.5	0.036	*
	Depth	472	2	24.9	3.5E-09	*
	Feature	407	3	14.3	1.4E-07	*
	Depth x Feature	122	6	2.1	0.057	
	Residuals	*776*	*82*			
Note:	*p<0.05					

Table 3. Pairwise (depth-feature) mean (±SE) substrate temperature (July 20 & July 22, 2014) and substrate moisture (June 15-17, 2014); *n* = 8 for each depth-feature mean.

	Temperature **Mean** (±SE)	**Moisture** **Mean** (±SE)
Depth-Feature		
Control-Bare	35.9 (±0.61)	37.7 (±0.58)
Deep-Bare	29.2 (±1.1)	32.2 (±0.68)
Shallow-Bare	41.5 (±0.7)	33.3 (±1.57)
Control-Log	29.5 (±1.4)	39.1 (±1.04)
Deep-Log	26.5 (±0.91)	32.9 (±1.65)
Shallow-Log	33.7 (±0.82)	35.6 (±1.51)
Control-Pebble Centre	30.3 (±0.42)	30.6 (±1.02)
Deep-Pebble Centre	26.6 (±0.45)	26.9 (±1.08)
Shallow-Pebble Centre	34.5 (±1.04)	32.1 (±1.75)
Control-Pebble Edge	31.8 (±0.78)	34.7 (±0.87)
Deep-Pebble Edge	28.4 (±0.53)	28.7 (±0.95)
Shallow-Pebble Edge	36.3 (±1.01)	36.5 (±1.03)

Table 4. List of mean germination rates (*n* = 3, for 26 species) obtained during the laboratory germination trial conducted on all plant species that were included in the Atrium green roof seed mixture.

	Mean % germination	SE
Forbs		
Anaphalis margaritaceae	87	1.7
Aquilegia canadensis	58	25.2
Atriplex spp.	93	1.7
Calystegia sepium	6	5.6
Campanula rotundifolia	15	15.0
Lathyrus maritima	20	5.8
Limonium carolinianum	21	3.3
Oenothera biennis	53	10.1
Prenanthes trifoliolata	0	0.0
Plantago maritima	47	6.7
Solidago sempervirens	40	15.3
Symphyotrichum novi-belgii	87	3.3
Shrubs		
Arctostaphylos uva-ursi	0	0.0
Empetrum nigrum	32	3.3
Empetrum eamsii	73	1.7
Gaultheria procumbens	72	10.9
Juniperus communis	0	0.0
Morella pensylvanica	0	0.0
Sibbaldiopsis tridentata	48	9.3
Vaccinium angustifolium	63	4.4
Vaccinium macrocarpon	100	0.0
Grasses		
Calamagrostis pickeringii	2	1.7
Danthonia spicata	97	3.3
Deschampsia flexuosa	70	8.7
Succulents		
Cakile edentula	25	15.0
Rhodiola rosea	60	5.8

Table 5. Incident rate ratios from negative binomial generalized linear models fitted to Atrium green roof mean seedling density data (*n* = 8, for 12 microsites) for June and September 2014; solar radiation (covariate, KWh/m^2) and microsite type (12 level factor) were included in the model; confidence intervals calculated from robust SEs; displayed as IRR (95% confidence interval).

	Seedling Density Mean (95% C.I.)	
	June	*September*
Microsites		
Control	1.5 (3.9, -1.0)	1.0 (3.7, -1.7)
Deep	6.0*** (8.8, 3.2)	5.8*** (8.9, 2.6)
Log Edge	2.2 (5.4, -1.0)	1.4 (5.3, -2.5)
Log Edge Deep	3.8*** (6.7, 0.9)	5.2*** (8.6, 1.8)
Log Edge Shallow	0.4 (4.7, -3.9)	0.6 (5.8, -4.6)
Pebble Centre	0.6 (3.4, -2.2)	1.4 (4.7, -1.8)
Pebble Centre Deep	2.0 (5.2, -1.2)	3.6** (7.0, 0.2)
Pebble Centre Shallow	1.4 (4.0, -1.2)	3.0* (6.0, 0.1)
Pebble Edge	2.3 (5.0, -0.5)	3.1** (6.3, -0.2)
Pebble Edge Deep	2.1 (6.2, -2.0)	3.6** (7.8, -0.6)
Pebble Edge Shallow	2.8** (5.7, -0.1)	3.5** (6.6, 0.4)
Shallow	0.0 (3.2, -3.2)	0.0 (3.5, -3.5)
Covariate		
Solar Radiation	1.0 (2.0, -0.004)	1.0 (2.0, -0.004)
Null deviance	180	161
Residual deviance	97	99
Observations	96	96
Log Likelihood	-189	-183
theta	1.8*** (0.5)	1.6*** (0.5)
Akaike Inf. Crit.	403.9	392
Note:	*p<0.1; **p<0.05; ***p<0.01	

Table 6. Incident rate ratios from Poisson generalized linear models fitted to Atrium green roof mean seedling species richness data (*n* = 8, for 12 microsites) for June and September 2014; solar radiation (covariate, KWh/m^2) and microsite type (12 level factor) were included in the model; confidence intervals calculated from robust SEs; displayed as IRR (95% confidence interval).

	Species Richness Mean (95% C.I.) *June*	 *September*
Microsites		
Control	0.8 (3.0, -1.5)	0.8 (3.0, -1.5)
Deep	3.1** (5.5, 0.7)	3.1** (5.5, 0.7)
Log Edge	1.6 (4.6, -1.4)	1.6 (4.6, -1.4)
Log Edge Deep	2.9** (5.3, 0.5)	2.9** (5.3, 0.5)
Log Edge Shallow	0.7 (4.4, -3.1)	0.7 (4.4, -3.1)
Pebble Centre	1.0 (3.5, -1.5)	1.0 (3.5, -1.5)
Pebble Centre Deep	1.8 (4.5, -0.8)	1.8 (4.5, -0.8)
Pebble Centre Shallow	2.1 (4.5, -0.2)	2.1 (4.5, -0.2)
Pebble Edge	2.2 (4.8, -0.4)	2.2 (4.8, -0.4)
Pebble Edge Deep	1.2 (4.3, -2.0)	1.2 (4.3, -2.0)
Pebble Edge Shallow	2.5* (5.0, -0.03)	2.5* (5.0, -0.03)
Shallow	0.000 (3.0, -3.0)	0.000 (3.0, -3.0)
Covariate		
Solar Radiation	1.0 (2.0, -0.003)	1.0 (2.0, -0.003)
Null deviance	115	144
Residual deviance	70	96
Observations	96	96
Log Likelihood	-116.6	-126.9
Akaike Inf. Crit.	259.3	279.7
Note:	*p<0.1; **p<0.05; ***p<0.01	

Figures

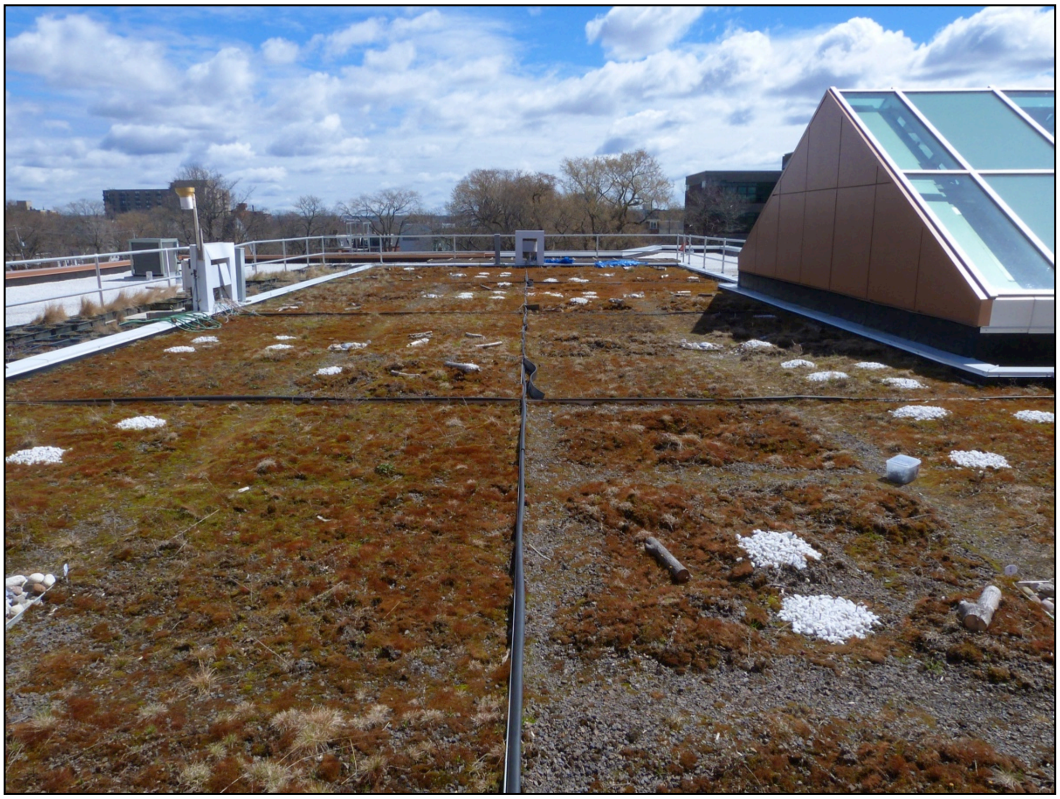

Figure 1. A photograph of the Atrium green roof with experimental depth and surface feature modifications, Halifax, Nova Scotia.

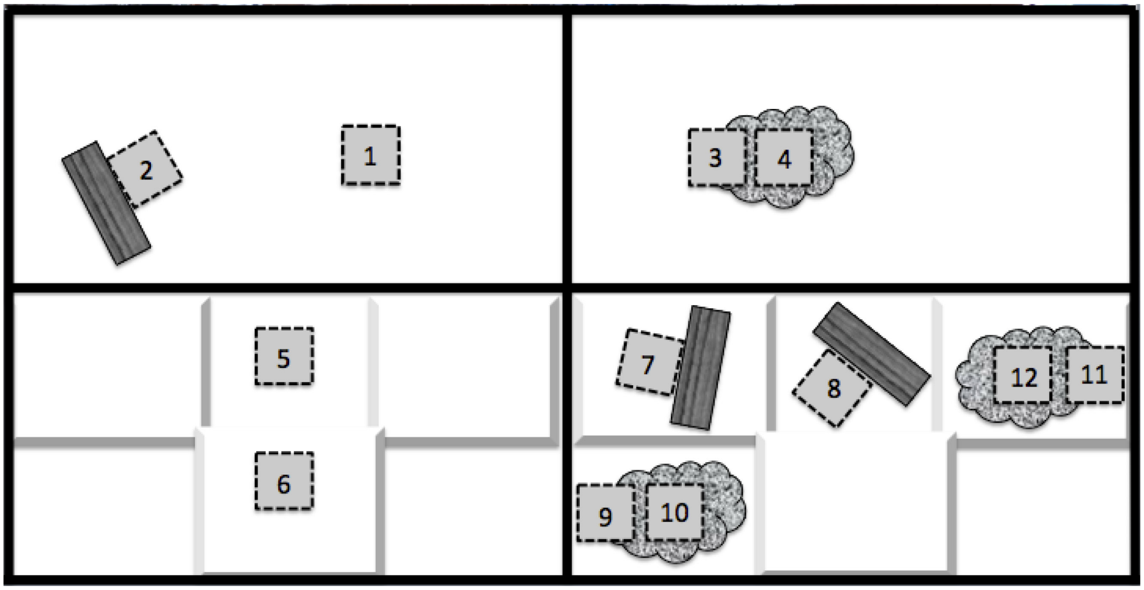

Figure 2. Diagram of green roof microsite locations relative to surface features (Bare, Log Edge, Pebble Edge, Pebble Centre) and substrate topography modifications (Shallow (2-3 cm), Control (7.5 cm), Deep (10-12 cm)). 1. Control-Bare, 2. Control-Log Edge, 3. Control-Pebble Edge, 4. Control-Pebble Centre, 5. Shallow-Bare, 6. Deep-Bare, 7. Deep-Log Edge, 8. Shallow-Log Edge, 9. Shallow-Pebble Edge, 10. Shallow-Pebble Centre, 11. Deep-Pebble Edge, 12. Deep-Pebble Centre.

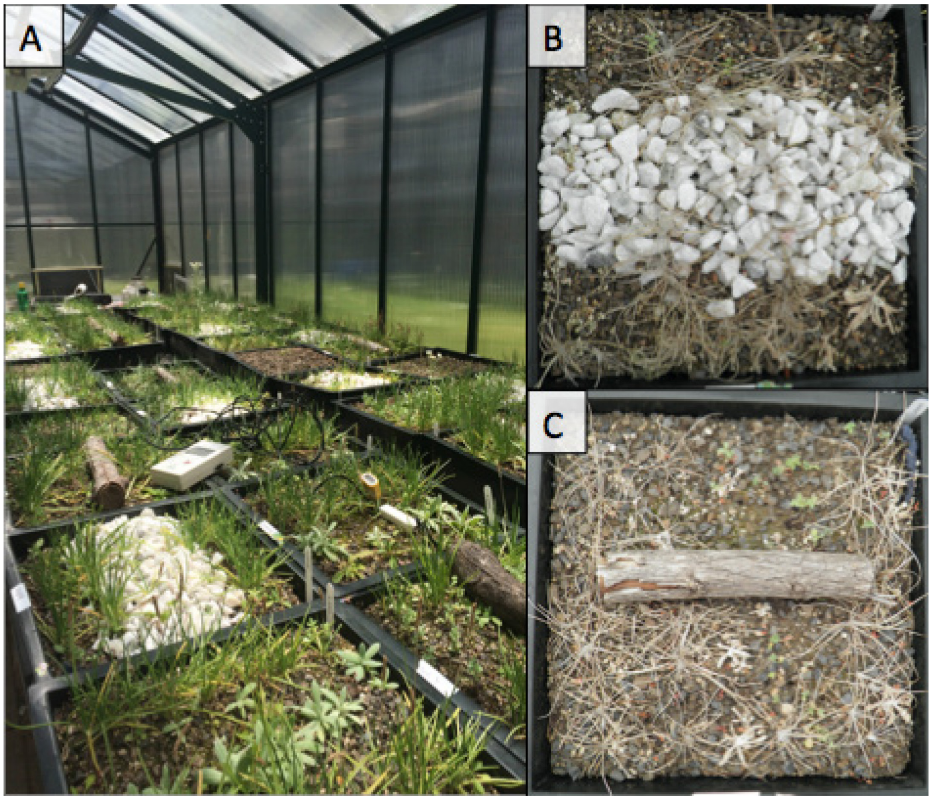

Figure 3. Photographs of the greenhouse experiment layout and heterogeneity treatments. *A* = Greenhouse layout, *B* = Pebble treatment, *C* = Log treatment.

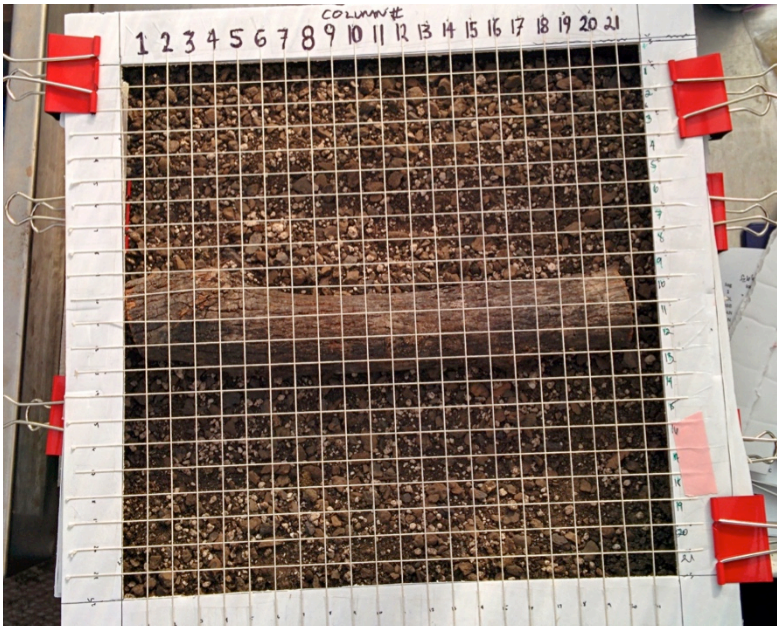

Figure 4. Photograph of the grid used to place seeds at precise locations in the greenhouse modules.

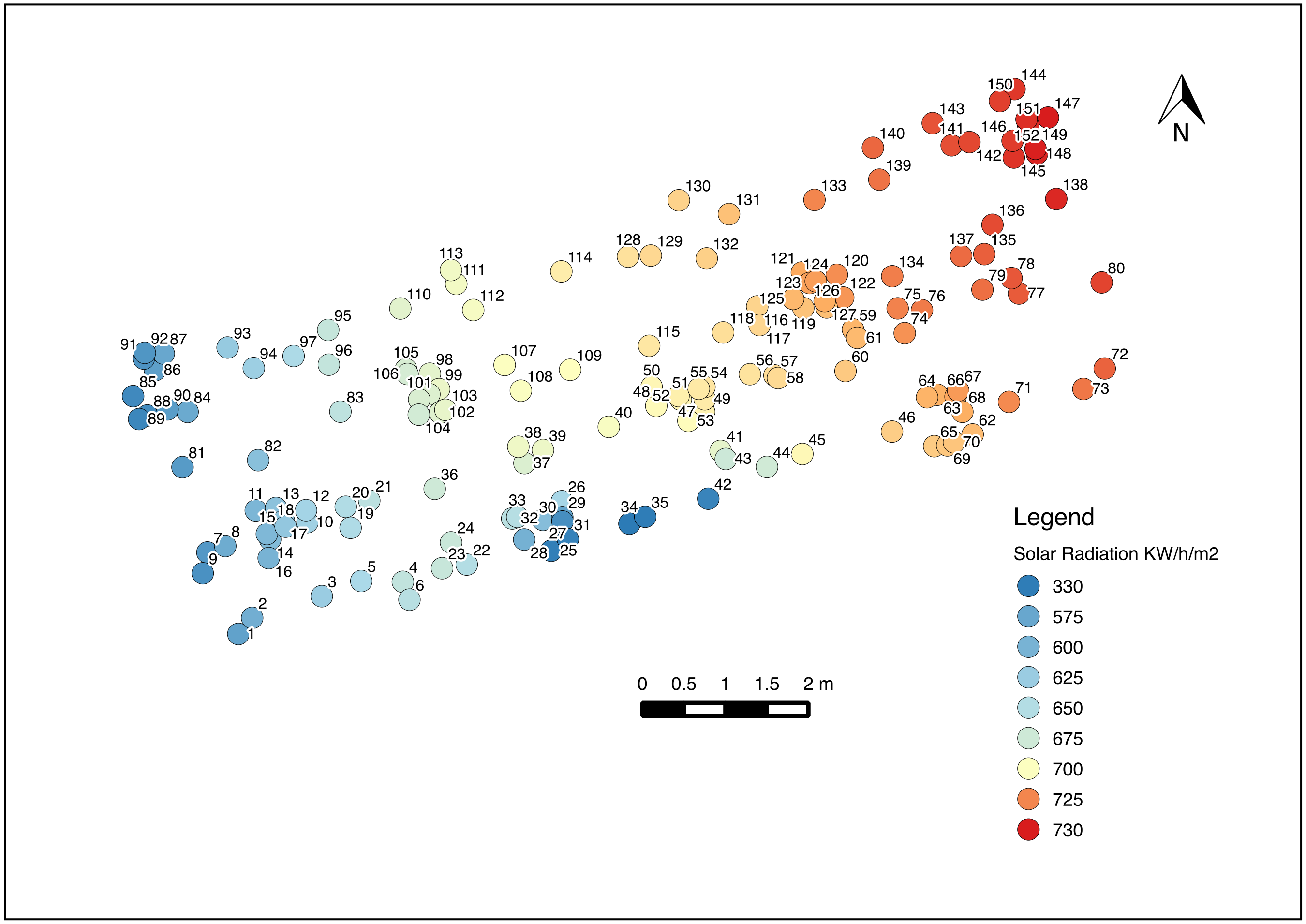

Figure 5. Map of modeled incident solar radiation (KWh/m^2) received by each quadrat on the Atrium green roof; values indicate total solar radiation at each quadrat location from May – September, 2014.

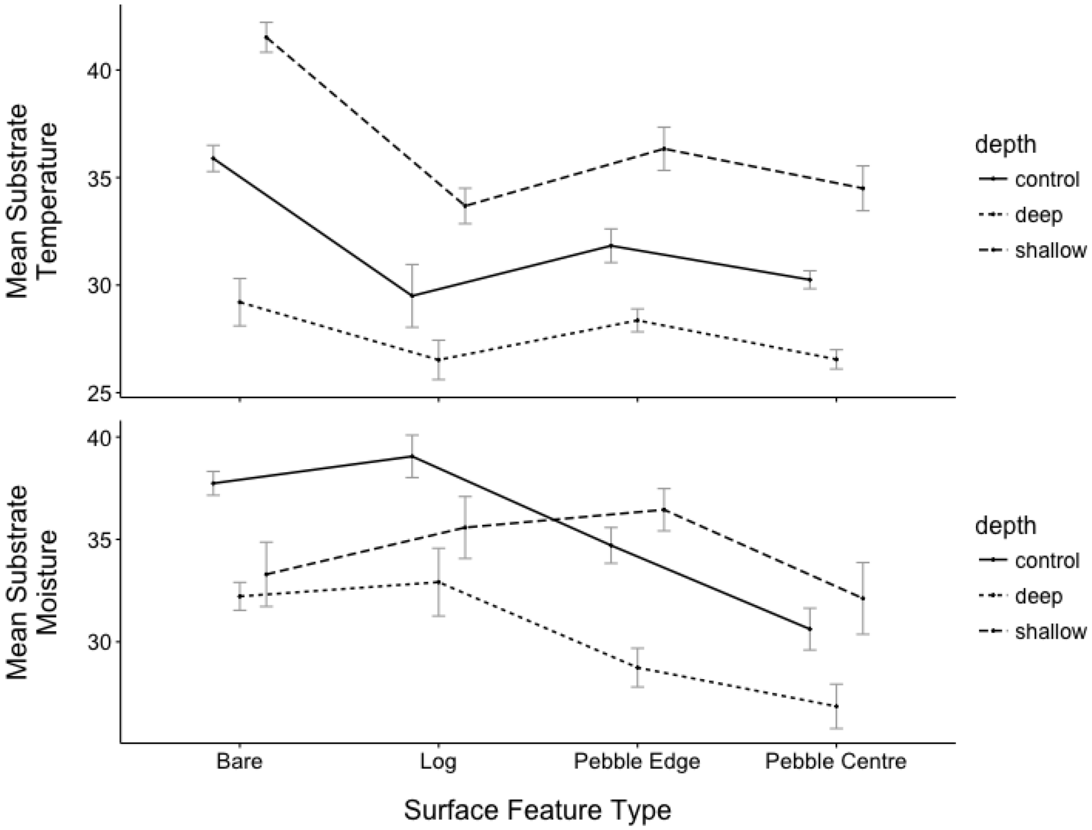

Figure 6. Mean (July 20 and 22, 2014) substrate temperature (°C) and mean (June 15-17, 2015) substrate moisture content (%) (*n* = 8, for 12 microsite types) according to soil depth and surface feature type; means adjusted for effect of total solar radiation and % vegetative cover. Error bars represent 1 standard error.

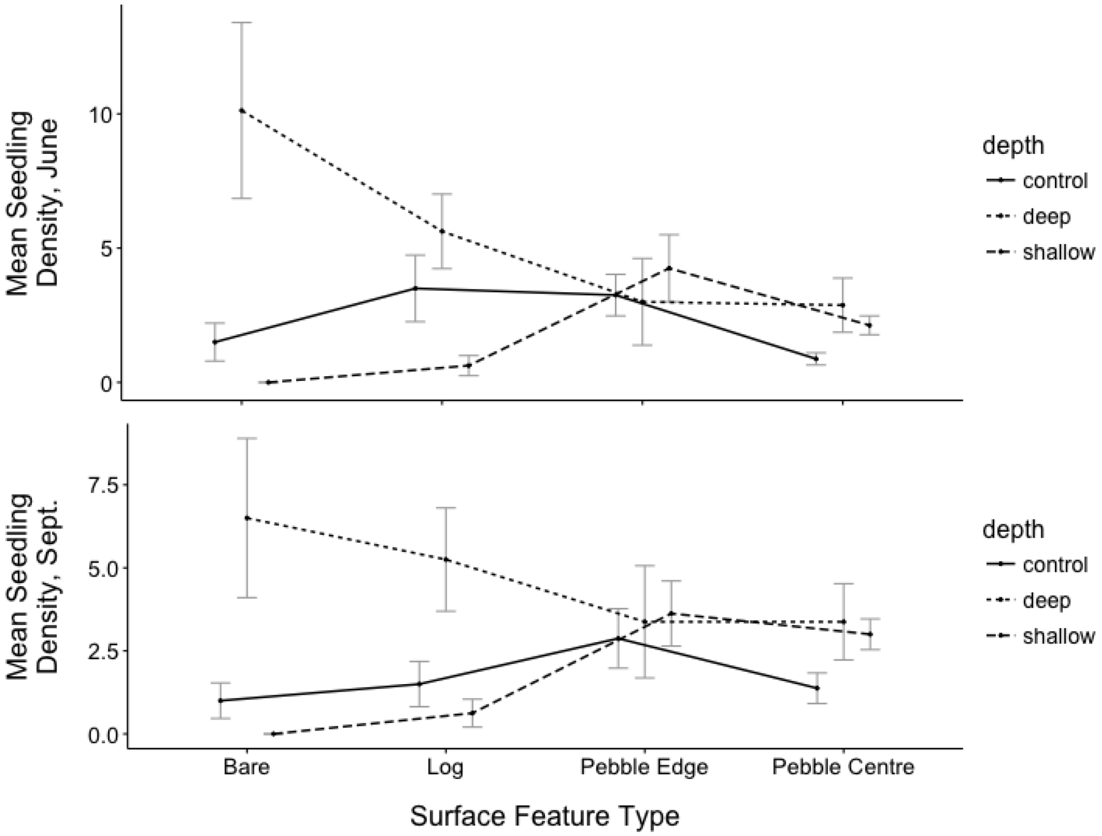

Figure 7. Mean seedling density in June and September (*n* = 8, for 12 microsite types) according to soil depth and surface feature type; means adjusted for effect of total solar radiation. Error bars represent 1 standard error.

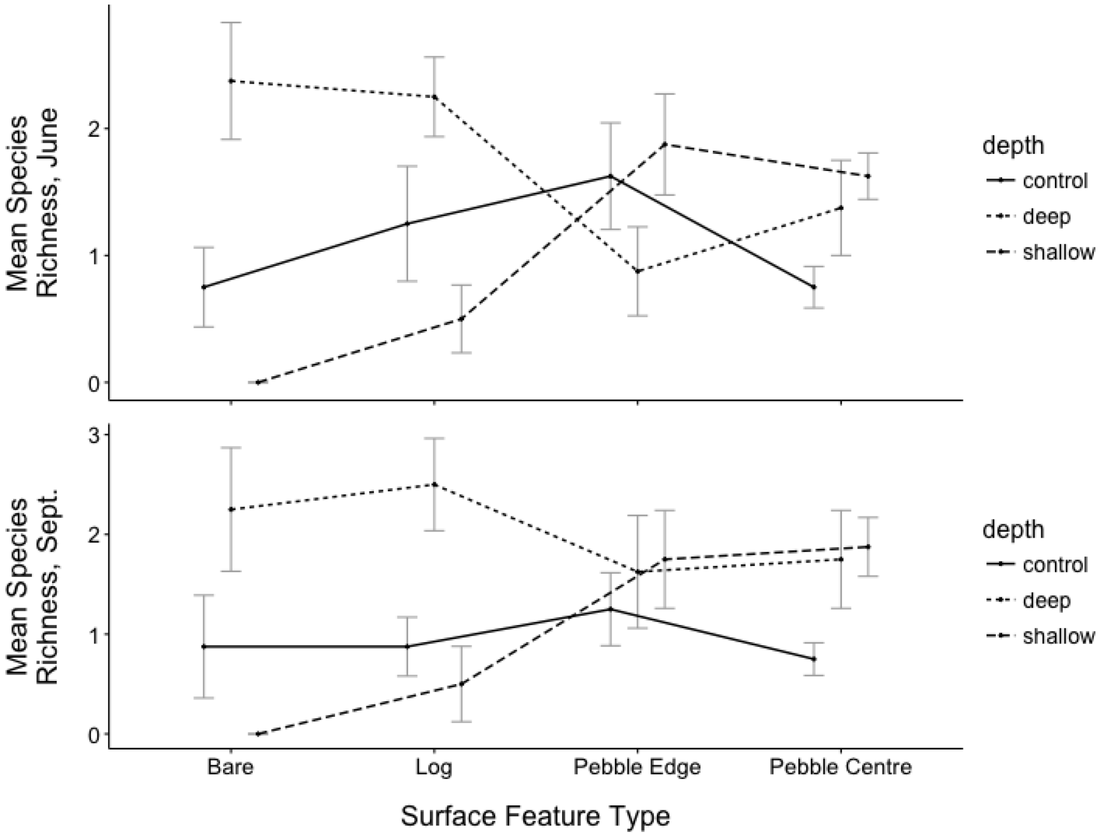

Figure 8. Mean seedling species richness in June and September (*n* = 8, for 12 microsite types) according to soil depth and surface feature type; means adjusted for effect of total solar radiation. Error bars represent 1 standard error.

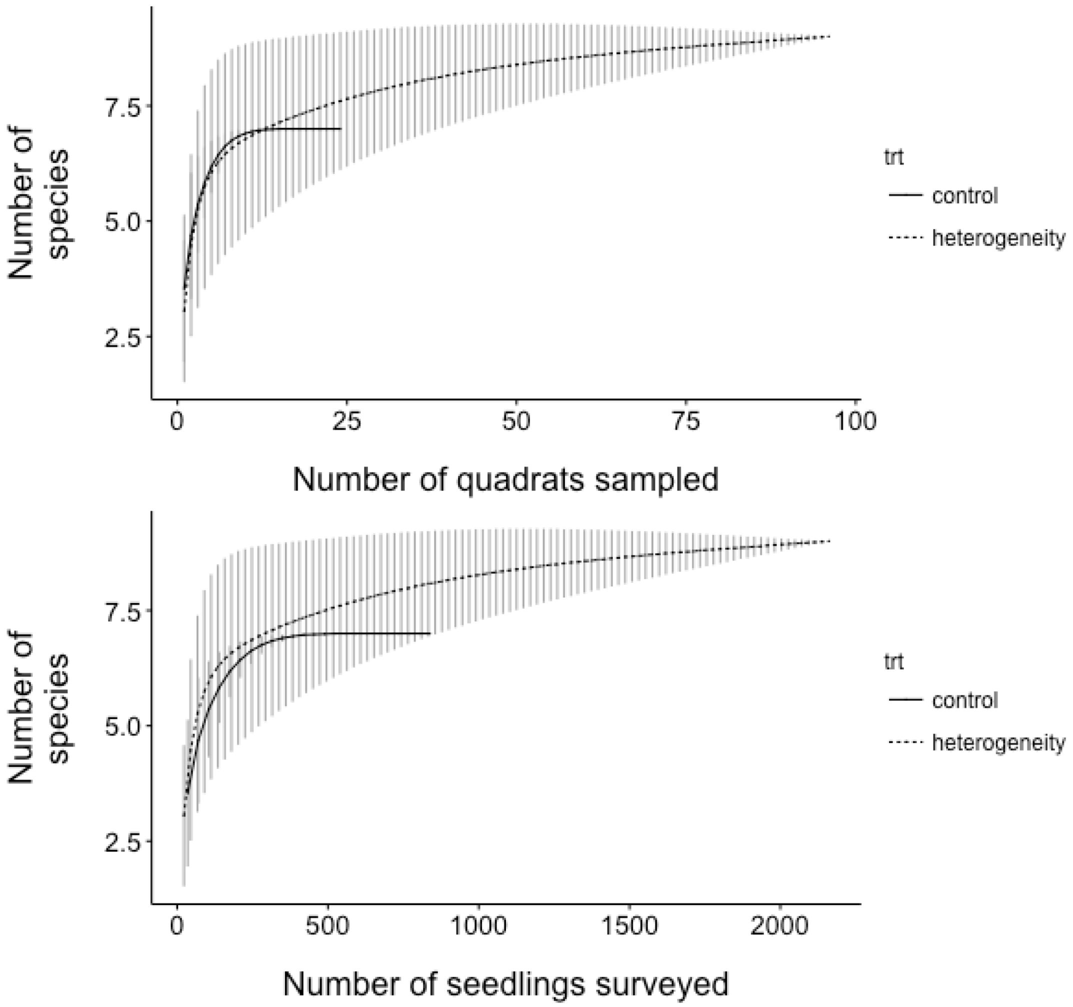

Figure 9. Sample-based and individual-based rarefied species richness curves comparing seedling community richness in heterogeneous (all unique (i.e. non-control) microsites combined, *n* = 96 quadrats) and homogeneous (seeded controls only, *n* = 24 quadrats) green roof environments. Bars represent 95% confidence intervals.

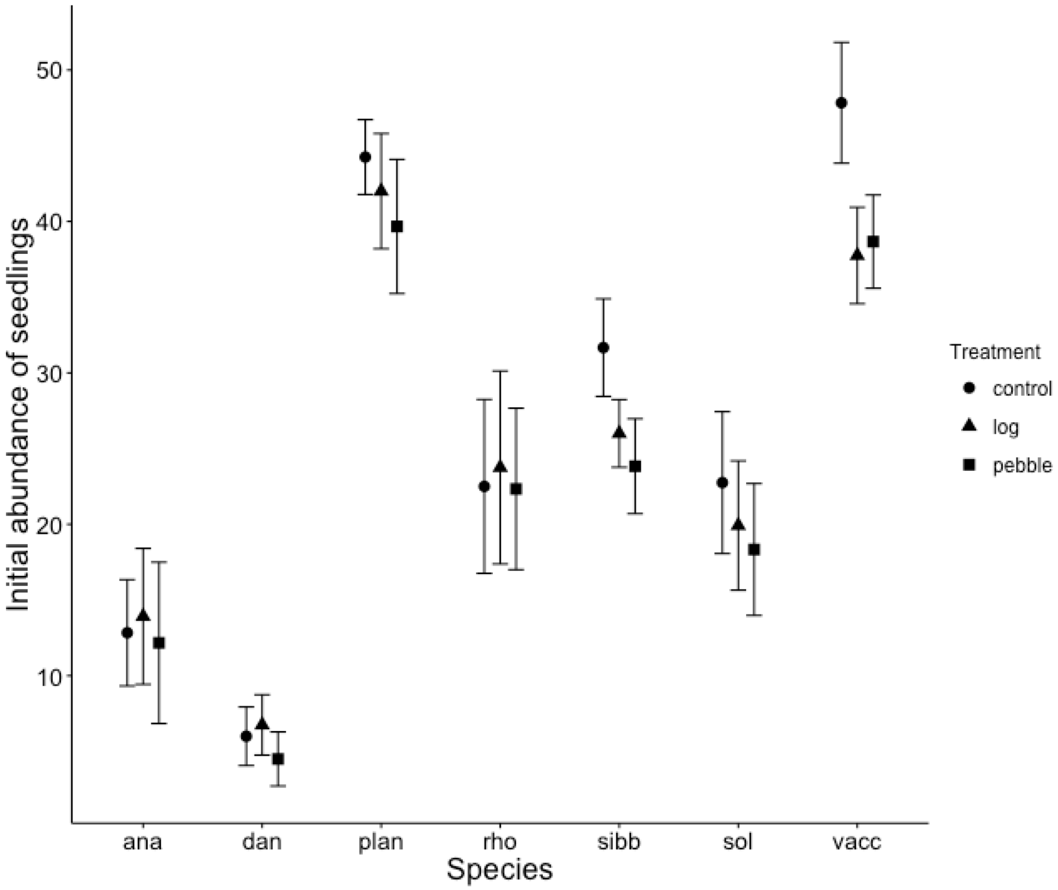

Figure 10. Mean and 95% confidence intervals of initial seedling abundance according to heterogeneity treatment and plant species, collected from the greenhouse experimental modules on drought day 0 (June 11, 2015).

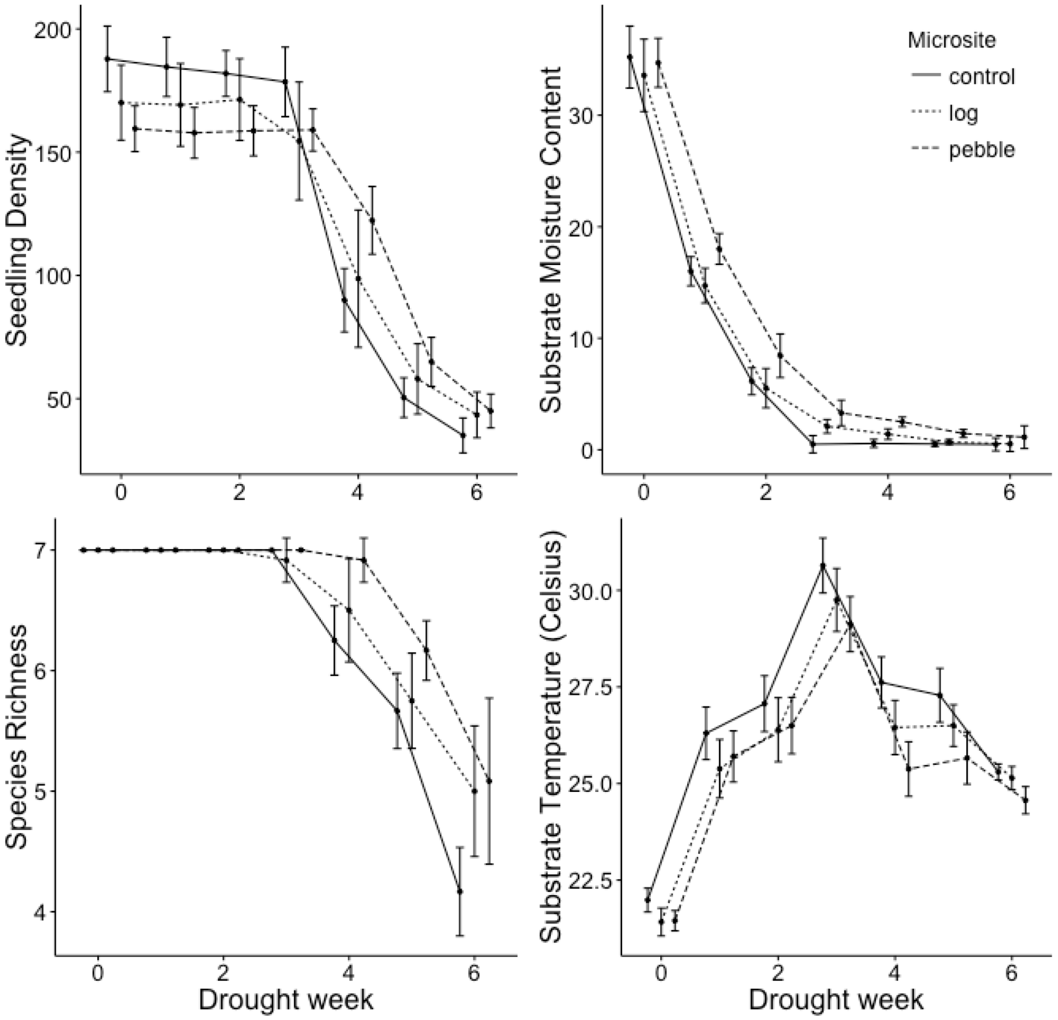

Figure 11. Means and 95% confidence intervals (*n* = 12, for 3 treatments) of seedling dynamics (species richness, seedling density) and substrate conditions (temperature, moisture content) over time (drought week), collected in greenhouse experimental modules June 11 – July 23, 2015.

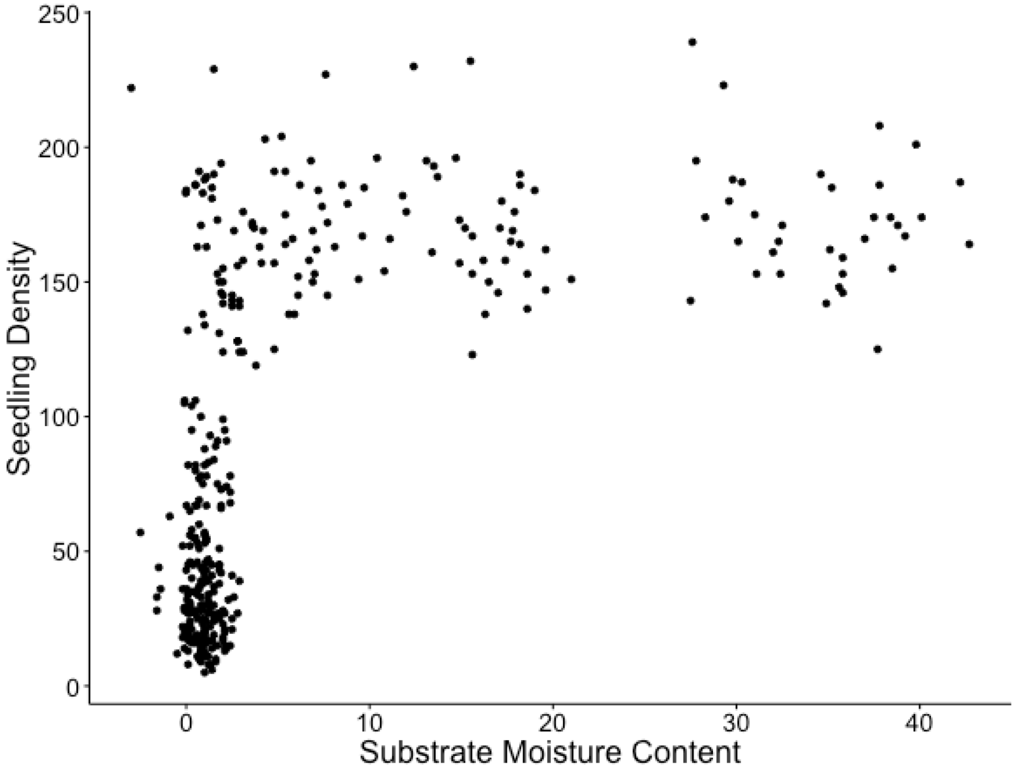

Figure 12. Seedling density according to substrate moisture content (%), collected from greenhouse experimental modules (*n* = 36, for 7 sampling periods) June 11 - July 23, 2015.

Chapter 3

“Wild bee community composition and pollen collection with ground level urban and coastal barrens comparisons”

Introduction

Ecosystem services are beneficial functions, such as decomposition or pest control, provided by natural ecosystems to humans. The process of urbanization erodes the ability of an ecosystem to provide these services (Grimm et al. 2008), which necessitates the provisioning of costly artificial services in cities (deGroot et al. 2010). In the 1970s, German researchers began investigating the potential for vegetated rooftops, or green roofs, to alleviate a suite of issues related to urbanization. Since then, many ecosystem services provided by green roofs have been catalogued, foremost being mitigation of stormwater runoff and reduction of building energy expenditure (Clark et al. 2008; Mentens et al. 2006; Oberndorfer at al. 2007).

Though these thermal and hydrological benefits have been well characterized following decades of research, the potential ecological benefits associated with green roof habitat provisioning for urban fauna, such as birds, bats, spiders, and insects, are less clear (Williams et al. 2014). Importantly, taxa likely to benefit from green roof habitat provide key services themselves; birds, bats, spiders, and wasps control insect pests, many ground-dwelling invertebrates decompose dead plant material and promote soil enrichment, and pollinators enhance reproduction of cultivated and wild plants (Hole 1981; Kearns et al. 1998; Klein et al. 2007; Lowenstein et al. 2015; Potts et al. 2010; Raupp et al. 2010). Few studies have examined green roof use by vertebrates (Baumann & Kasten 2010; Coffman & Davis 2005; Pearce & Walters 2012); however, researchers in Switzerland (Brenneisen 2006; Braaker et al. 2013), England (Jones 2002; Kadas 2006; Rumble & Gange 2013), Germany (Schrader & Böning 2006), France (Madre et al. 2013), the United States (Tonietto et al. 2011; Ksiazek et al. 2014), and Canada (Colla et al. 2009; MacIvor & Lundholm 2011a; MacIvor 2015; MacIvor et al. 2015) have characterized arthropod colonizers of green roofs, with early studies confirming the ability of green roofs to support a variety of arthropod taxa, including some rare and specialist species (Brenneisen 2006; Jones 2002; Kadas 2006; Schrader & Böning 2006).

Comparisons of arthropod richness and abundance at urban ground level and green roof locations followed these general surveys. Two studies (Colla et al. 2009; Tonietto et al. 2011) reported lower abundance and richness of green roof bee communities relative to ground level habitat, though work by MacIvor and Lundholm (2011a) revealed no differences in abundance or richness of multiple invertebrate taxa between rooftop and ground level sites. Research by Rumble and Gange (2013) highlighted the taxonomic impoverishment of soil arthropod communities on green roofs in England, dominated by drought-tolerant collembolans and mites. Being flightless, these soil arthropods would be expected to exhibit high fidelity to a given roof and a reliance on rooftop resources. The low taxonomic diversity and highly unstable population sizes observed by Rumble and Gange indicate that green roofs may not represent high quality habitat for some low-mobility arthropod populations.

While low-mobility invertebrates may perceive green roof environments as stressful, others with greater mobility, such as bees, flies, and butterflies, may not. Many pollinators are highly mobile and observation or capture on a green roof does not imply usage of specific green roof floral or other resources. Though the habitat provisioning by green roofs for these mobile taxa remains unclear, it appears that the plants growing on green roofs can benefit from visitation by these groups. Work by Ksiazek and co-workers (2012) suggests that pollination by specific taxa facilitates reproduction of green roof forbs, which produced high quality seed similar to that of ground level conspecifics in Chicago (Ksiazek et al. 2014). However, few studies have explicitly linked pollinator communities to specific food or nesting resources provided by green roofs (Ksiazek et al. 2012; MacIvor et al. 2015). The habitat value of green roofs for mobile invertebrate taxa will remain ambiguous without quantitative assessments of the specific resources provisioned by green roofs and used by visiting invertebrates.

Given their mobility and presence in urban environments, bees are potential beneficiaries of habitat provided by green roofs; in return, bees offer substantial support to flowering plants through their facilitation of cross-pollination. Though many attribute pollination services to imported honeybees (*Apis mellifera*), native bees outperform honeybees as pollinators by employing more diverse pollen harvesting techniques and by increasing flower visitation rates (Garibaldi et al. 2011; Garibaldi et al. 2013; Javorek et al. 2002; Vázquez et al. 2005; Winfree et al. 2010). However, native bee populations can exhibit significant annual fluctuations in size, displaying variations in abundance of up to 300% between years (Roubik 2001). Despite these fluctuations, pollination services provided by wild bees contribute significantly to commercial crop production (Klein et al. 2007; Potts et al. 2010), with fruits and vegetables demonstrating a strong reliance on these pollinators (Gallai et al. 2009).

The severity of recent honeybee losses, related to severe weather, pesticide use, mite infestations, fungal diseases, and reduced habitat area containing alternative forage plants (vanEngelsdorp & Meixner 2010), underscores the importance of diverse crop pollinator communities (Ghazoul 2005). Recent analysis demonstrated that in the United States, 39% of farmland planted with pollinator-reliant crops is located in regions that show low bee abundance (Koh et al. 2016). Increasing awareness of the value of native bees to cultivated and wild plant reproductive success has motivated multiple investigations of native bee population trends. Sustained population declines have not been observed in all native bee species (Ghazoul 2005), although significant declines in species richness were observed in many British and Dutch bee communities surveyed from 1980-2005 (Biesmeijer et al. 2006). Half of all bumblebee species in North America appear to be in decline relative to historical population sizes of the 1930s and 1960s, though others appear to be increasing or have remained stable within historical population levels (Colla et al. 2012). Bumblebee species with the smallest ranges appear most vulnerable to population decline, with some species displaying precipitous declines in population size (Colla et al. 2012). Habitat loss is the primary driver of bee decline, though climate change is also likely to promote phenological asynchonies between bees and their host plants (Potts et al. 2010; Winfree 2010).

Though habitat degradation has negatively affected bee populations, certain bees appear to be adapted to life in urbanized areas; some bee communities respond positively to moderate human disturbance and studies along urban-rural environmental gradients indicate that urbanization does not always effect a decrease in overall bee species richness (Cane et al. 2006; Verboven et al. 2014; Winfree et al. 2007). Responses vary among bee taxa (Cariveau & Winfree 2015); small-bodied bees, such as *Lasioglossum*, appear frequently in urban bee surveys (Colla & Packer 2008; Fetridge et al. 2008; Matteson et al. 2008; Packer et al. 2007; Sirohi et al. 2015) while members of Colletidae and Andrenidae are typically underrepresented (Hernandez et al. 2009). Cavity-nesting bees appear to increase in abundance in response to the urbanization of multiple landscape types (Hernandez et al. 2009), and research by McFrederick and LeBuhn (2006) revealed bumblebees exhibited greater species richness at urban sites relative to those located in a natural landscape, likely due to reductions in competitive exclusion.

The positive response to urbanization exhibited by some taxa suggests that habitat management efforts focusing on cities may benefit wild bee conservation and could potentially augment pollinator visitation to agricultural fields adjacent to urban gardens. Pereira-Piexoto and co-workers (2014) found that bees nesting in urban gardens collected pollen in agricultural fields during the peak bloom of cultivated rapeseed (*Brassica napus*), demonstrating pollinator 'spillover' at the urban-rural interface. The movement of pollinators between urban and rural landscapes could augment pollination services provided to urban and peri-urban agriculture. The benefits from bees undertaking urban-rural commutes could be substantial given that, globally, 60% of all irrigated farmland and 35% of all rainfed farmland is located within 20 km of an urbanized area (Thebo et al. 2014). Furthermore, of those urban areas with populations exceeding 50,000 people, 98% contain at least some cropland within city boundaries, with low-income inhabitants in developing countries relying most heavily on production from urban agriculture (Thebo et al. 2014).

Overall, diverse and abundant garden forage and heterogeneous nesting sites appear to support urban bee populations (Cussans et al. 2010; Pereira-Piexoto et al. 2014), and it has been suggested that green space (including gardens and parks) within urbanized areas may serve as refugia for certain bumblebee species (Cussans et al. 2010; Goulson et al. 2010). One British study revealed an increase in *B. terrestris* weight gain in urban habitat relative to farmland (Goulson et al. 2002). Thus, well-provisioned gardens may attract and support many bee taxa living in an urbanized environment, and increasing the total garden area planted with native species can draw more bees to these urban gardens (Fukase & Simons 2016). Certain wildlife gardening techniques, such as provisioning of solitary bee boxes, may increase bee diversity in urban yards (Gaston et al. 2003), attracting both native and non-native bees and wasps (MacIvor & Packer 2015).

Because the maximum foraging distances displayed by some solitary bees are short, they respond to local habitat features, such as those incorporated into backyard gardens (Gathmann & Tscharntke 2002). Wild bees are central-place foragers that return to their nest after travelling to collect nectar and pollen from suitable hosts in flower. Maximum foraging neighbourhood size varies by bee species, though few individuals actually forage to the edge of their range–rather, most bees will visit flowers no more than 300 m from their nest site (Zurbuchen et al. 2010). Shwartz and co-workers (2013) found that small-scale management programs aimed at improving public-garden biodiversity had a greater impact than landscape scale efforts in Paris, France. However, Matteson & Langellotto (2011) found that the introduction of native species on a similar scale did not alter beneficial insect richness, as many of these insects were attracted to exotic plant species in gardens. For example, *Trifolium,* an exotic legume that frequently colonizes urban lawns in Canada, provides protein-rich pollen and is consequently visited by many native bees (Larson et al. 2014). Some urban cavity nesting bees have displayed remarkably homogeneous pollen usage when provisioning brood cells, relying heavily on clover and tree pollen available in Toronto (MacIvor et al. 2014). Regardless of nativity, plant diversity and floral abundance have been shown to correlate with bee diversity within cities (Hennig & Ghazoul 2012).

Attraction of wild bees to urban gardens can result in significant benefits for garden species. Lowenstein and co-workers (2015) found that higher rates of visitation and a greater diversity of bee visitors augmented both fruit and seed set in common garden plants. Research by Cussans and co-workers (2010) demonstrated that fruit set of *Lotus corniculatus* and *Glechoma hederacea* was increased in gardens relative to farmland, and Verboven and co-workers (2012) observed that pollinator visitation rates to *Digitalis purpurea* were similar in urban gardens and natural reference sites. However, greater forage diversity in cities may dilute intraspecies pollen transfer; Leong and co-workers (2014) found that reproduction of a weedy species, *Centaurea solstitialis*, was reduced in urban locations despite greater bee visitation rates relative to rural sites.

Many of the weedy, spontaneously colonizing cosmopolitan plant species adapted to urban habitats (McKinney 2006) may compete with garden plants or urban crops for bee visitation, attracting generalist pollinators away from other species or displacing higher quality or preferred floral hosts typically present in the landscape (Potts et al. 2010). The generalized foraging strategies exhibited by most urban bees would allow them to use the heterogeneous floral resources provided by urban vegetation, as urban bee communities contain few, if any, specialists (Hernandez et al. 2009). The role of urban weeds (such as *Taraxacum officinale)* may be particularly important in early spring and late fall, when few garden plants are in bloom – providing supplemental nectar and pollen during periods of resource scarcity (Sirohi et al. 2015). Phenological complementarity of flowering species between habitat types has been shown to support bee diversity in anthropogenically-modified environments (Mandelik et al. 2012). Through temporal resource complementarity, diverse landscapes can promote greater bee diversity, supplying attractive floral resources across the entire summer (Mallinger et al. 2016).

Winfree and co-workers suggested that the response of a bee community to changes in land use may be nested within its response to modifications of overall flower provisioning across a landscape gradient (Winfree et al. 2011). Gardens appear to fulfill the habitat requirements of some bees (Frankie et al. 2005; Goulson et al. 2002; McFrederick & LeBuhn 2006), but locations close to the urban core may offer fewer ground level resources for foragers. Though bees may rely on weedy, spontaneous vegetation for resources in these developed areas, private and municipal weed management programs may reduce resource availability, and public support for programs encouraging weedy vegetation would likely be low.

Green roofs offer an alternative means of increasing floral resource abundance in heavily developed areas. Urban bees may benefit from the pollen and nectar offered by rooftop vegetation and from the intense solar exposure that characterizes green roofs, as bees prefer to forage in open, sunny spaces and appear to respond positively to floral area and sun exposure regardless of surrounding green space extent (Matteson & Langellotto 2010; Michener 2007, p. 4). Even in less developed areas, intense competition for resources at ground level manifests through depleted nectar and reduced pollen availability; this may lead to the exclusion of some species. Bumblebees have been shown to alter their foraging behaviour in the presence of competing congenerics (Inouye 1978). Green roofs might offer alternative forage for less competitive taxa, as Sowig (1989) found that resource sharing among bumblebee species occurred when visitors could choose among different forage patch sizes.

Furthermore, the potential attractiveness of native plants in urban settings (Fukase

& Simons 2016) suggests that native-planted green roofs may offer unique resources not typically found in ground level gardens and may even attract bees not commonly found within the urban matrix. However, the role of native-planted green roofs in provisioning nectar and/or pollen to urban bees remains unknown. In Toronto, wild bees foraging on a green roof planted with exotic *Sedum spp.* appeared to collect large amounts of *Sedum* pollen during peak bloom (MacIvor et al. 2015), but no research has determined the extent to which urban bees collect pollen from locally-sourced native plants growing on green roofs.

Researchers in Halifax have evaluated a suite of locally occurring native plant species suited to the growing conditions present on shallow-substrate green roofs (MacIvor & Lundholm 2011b). Successful plants have been sourced from coastal barrens habitat, characterized by highly variable weather conditions, near absent tree canopy cover, and fluctuating soil moisture conditions (Cameron & Bondrup-Nielsen 2013; Oberndorfer & Lundholm 2009; Porter 2013). Plant communities in these environments tend to be dominated by ericaceous shrubs, and surveys indicate that this habitat type hosts several rare plant species (Oberndorfer & Lundholm 2009; Porter 2013).

While investigations of barrens vegetation assemblages and associated environmental characteristics have been completed, no surveys of coastal barrens bee fauna have been conducted in Nova Scotia. Without a description of coastal barrens bee fauna, assessments of associations between coastal barrens plant species and wild bee species on native-planted green roofs would be incomplete. Therefore, my research aimed to describe the bee fauna of coastal barrens locations within the Halifax Regional Municipality, and to compare these bee communities to those found within the city at ground level and green roof locations that contained two native barrens plant species, *Sibbaldiopsis tridentata* and *Solidago bicolor.* To examine direct use of green roof resources by native bees, pollen load analysis was conducted on bumblebees (*Bombus spp.*) collected during the flowering period of *S. bicolor* at green roof, ground level urban, and coastal barrens sites. I predicted that bee communities would be most abundant and species rich in coastal barrens, moderately abundant and species rich at urban ground level sites, and least abundant and species rich at urban green roof sites. I further predicted that bee community composition would differ between urban and coastal barrens locations, and that green roof bee communities and their pollen load contents would most closely resemble those of ground level urban sites.

Methods

Sites

During two sampling periods in 2014, wild bees were collected from three site types representing green roof, urban ground level, and coastal barrens locations within the Halifax Regional Municipality, NS (Table 1). Two locations were sampled within each site type during each collection day (six locations per day), except where noted. The collection periods coincided with the flowering period of two native plant species, *Sibbaldiopsis tridentata* and *Solidago bicolor,* which have established and spread successfully on an experimental green roof in Halifax and which occur in plant communities in local coastal barrens habitat. *S. tridentata* is a perennial creeping shrub with white, five-petaled, perfect flowers arranged in branched cymes; it flowers from June to July (Munro et al. 2014). *S. bicolor* is a perennial forb with a terminal multi-flower capitulescence (10-15 cm in length) of small, centrally located yellow, perfect disk flowers surrounded by white, pistillate ray flowers, which blooms August to September (Munro et al. 2014). The first bee collection period (June 23 – 25, June 28 – 29, July 2, 2014) occurred while *S. tridentata* was in bloom at all sites, the second (August 5, 11–12, 2014) while *S. bicolor* was in bloom.

Bees were collected at a total of seven sites over the summer; these sites were selected based on the presence of the two focal plant species and the classification of each location as either urban or barrens in the Spatially Related Forest Resources (SRFR) information system, maintained by the Nova Scotia Department of Natural Resources (NSDNR 2015) (Table 1, Figures 1-2). These site requirements significantly limited the number of sites available for monitoring: within Halifax Regional Municipality (HRM), only two native-planted green roofs including both floral hosts were identified (one at the Nova Scotia Community College (NSCC green roof), the other at Saint Mary's University (Atrium green roof)), and urban ground-level sites containing >5 individuals of either focal host species were also difficult to locate – two urban ground level sites (Pine Hill and Point Pleasant Park) were found to contain *S. tridentata*, but only one site in urban HRM (Pine Hill) contained >5 individuals of *S. bicolor*.

Visual pedestrian surveys were completed to develop a list of flowering plant species present at each collection location (Tables 2-7), to provide an estimate of floral diversity available to bees and to identify possible sources of pollen. These surveys included plants flowering within 250 m of the bee collection areas and were conducted before, during, and after the bee sampling periods to ensure that both early and late blooming species were identified. Plant species were identified using Nova Scotia Plants (Munro et al. 2014) and Roland's Flora of Nova Scotia (Roland & Zinck 1998) and nativity was determined using these texts and the conservation status ranks produced by the Atlantic Canada Conservation Data Centre (ACCDC 2014).

Two green roofs containing the focal plant species were sampled over all collection periods (Table 1, Figures 1-2). The Atrium green roof is located on Saint Mary's University campus in Halifax, NS. This green roof consists of a 216 m^2 rectangular vegetated area on the fifth story of the Atrium building; it was installed in 2010 and has since been covered primarily by *S. tridentata*, *S. bicolor*, *Danthonia spicata*, mosses, and lichens; other forbs and grasses have dispersed into the vegetated area from adjacent modular experiments. Weeds have been periodically removed, though this maintenance activity ceased during the study period. The roof receives uneven shade from surrounding buildings. The second green roof included in this study is located at the NSCC waterfront campus in Dartmouth, NS, over the Centre for the Built Environment, and features a vegetated area of 75 m^2 approximately eight meters above ground level, installed June 2013. The NSCC green roof plant community is composed of ten species of *Sedum* and mixed plantings of native species (*S. bicolor*, *Campanula rotundifolia, Sagina procumbens, Rhodiola rosea, Luzula multiflora, Plantago maritima, Danthonia spicata, Deschampsia flexuosa, Festuca rubra,* and *S. tridentata*). Installation details are described by Appleby-Jones (2014). One quarter of the roof area is planted exclusively with *Sedum*, while the remaining roof area contains a patchwork of *Sedum* plots and native species plots. Twenty modules containing *S. bicolor* in flower were transported to the site in late July to facilitate bee collection in August, as few *S. bicolor* individuals were present within the vegetated area. A smaller green roof was located one level above this study roof, and the plant species present on this smaller roof were included in the site floral survey.

Two urban ground level sites were included in this study, both occurring on the Halifax peninsula (Table 1, Figures 1-2). One site (Pine Hill) was located in a residential area of Halifax on Pine Hill Drive and was sampled during the bloom period of both focal host plant species. This site features plants common to coastal barrens, including *Empetrum*, *Aronia*, *Ilex, Morella,* and *Vaccinium,* as well as common city weeds, such as *Hieracium* and *Vicia*. Surrounding properties contained garden ornamentals, herbs, and weeds. An additional ground level urban site was located in Point Pleasant Park. This approximately 75-hectare park (Jotcham et al. 1992) hosts popular walking trails and a mixed forest community, which experienced significant disturbance in the form of blowdown damage in September 2003 as a result of Hurricane Juan (Burley et al. 2008). Surveys of park vegetation (Burley et al. 2008; Neily et al. 2004) revealed a diverse plant community within the park, including many understory species atypical of the urbanized peninsula. Both urban sites featured numerous weedy plant species. Only the site at Pine Hill contained both *S. tridentata* and *S. bicolor*; therefore Point Pleasant was not sampled in the later (August) collection period. Rather, the site at Pine Hill was sampled for three additional days (August 6-8, 2014) during which no other sites were sampled.

Bees were collected at three coastal barrens sites, Chebucto Head, Herring Cove, and Prospect (Table 1, Figures 1-2). These habitats are exposed to high winds and solar radiation, due to their proximity to the ocean and near absence (> 25%) of forest cover; weather conditions in these exposed coastal locations can fluctuate significantly within a day (Neily et al. 2005; NSDNR 2006). Coastal barrens, or coastal heathlands, are characterized by low-growing and shrubby plant communities dominated by ericaceous species, such as *Empetrum nigrum*, *Kalmia angustifolia*, *Morella pensylvanica*, and *Vaccinium angustifolium*, though plant community composition can vary significantly among sites (Cameron & Bondrup-Nielsen 2013; Oberndorfer & Lundholm 2009; Porter 2013). While *S. tridentata* occurs at all three barrens sites, *S. bicolor* was located only at Chebucto Head and Herring Cove. Accordingly, Chebucto Head and Prospect were sampled in the early (June) collection period, while Chebucto Head and Herring Cove were sampled during August. The coastal barrens at Herring Cove are spread thinly between a rocky coastline and a forested inland border that abuts a coastal road, whereas the barrens at Chebucto Head and Prospect are comparatively open (Figure 1). Paved areas interrupt the Herring Cove and Chebucto Head barrens; exotic plants (*Centaurea, Trifolium*) often populate the margins of these features along with more typical barrens taxa.

Pollen and bee collection

To facilitate later pollen identification, individual pollen samples were collected from all plant species flowering within 50 m of each plot (though the reference pollen collection area was reduced at the Pine Hill site due to the proximity of private residences). A synoptic pollen collection was thus developed for co-flowering species at all sites. Pollen was collected in the field on fuchsin-stained glycerin jelly (according to Kearns and Inouye (1993)); reference pollen slides were mounted and sealed on the day of pollen collection or frozen until mounting could be completed. Images of representative pollen grains for all reference species were taken at 40x or 63x magnification, depending on grain size. These images constitute the visual pollen library that was used during pollen identification.

Bee collection effort was standardized by area, sampling duration, collector effort, and collection day. Based on the footprint of the smallest green roof sampled (NSCC), a single 9.7 m x 7.7 m permanent plot was established at all sampling locations. Following a thorough pedestrian survey of each site, the plots were positioned to include the focal plant species. The number of flowers of the target plant species (*S. tridentata*) or the number of target plants (*S. bicolor*) present at the sites was recorded on each sampling day. Timed aerial netting of wild bees was conducted between 10 a.m. and 4 p.m. Each day, two collectors monitored a given sampling plot for one hour and netted all observed bees that landed within the plot. The plant species (or non-floral feature) on which the bee alighted prior to capture was recorded; if the plant species was not known, the plant was photographed or tagged and later identified. Netted bees were transferred to individual cleaned vials to reduce pollen contamination and were frozen on the day of capture. Bees were stored in a commercial freezer prior to preparation and pinning and were returned thereafter.

Specimen preparation and identification

Pollen

As many more bumblebees were collected at ground level locations relative to green roofs, only those bumblebees collected in August were subjected to pollen analysis to avoid further unbalancing the sample size for each site type. Bumblebee pollen was removed manually using insect pins (one pin per specimen) in preparation for subsequent microscopic inspection. Residual pollen was removed by vortexing bees individually for

60 seconds in cleaned vortex tubes filled with 15 mL 70% ethanol; the solution was poured through a #2 cone coffee filter. This process was repeated three times for each bee to optimize pollen yield. Filters were covered and dried in a fume hood; pollen was scraped from the filters with forceps and combined with the previously collected pollen. Pollen loads for each bee were stored on fuchsin-stained glycerin jelly in microcentrifuge tubes and frozen prior to mounting to suppress germination. Glycerin jelly was made according to Kearns and Inouye (1993). Pollen preparation techniques were adapted from Jones (2012) and Kearns and Inouye (1993). Tubes containing bee pollen samples and glycerin jelly were warmed in a 70°C water bath; 100 µL distilled water was added to the melted jelly to reduce viscosity. For each sample, 10 µL subsamples of the glycerin jelly-pollen mixture were mounted in triplicate on cleaned microscope slides, covered with coverslips, and sealed with clear nail polish.

Pollen was identified using the reference pollen image library, Crompton and Wojtas (1993), Girard (2014), and the PalDat online palynological image database. Triplicate subsamples were visually compared to determine sample homogeneity. A single subsample was assessed for each specimen once between subsample homogeneity was achieved. All morphotypes present were identified and enumerated up to 100 grains. Morphotypes were classed as ‘dominant’ if 100 grains or more were counted in a subsample. For each slide, the total number of morphotypes and the identity (to species or type group, e.g. *Mentha*-type) and grain count for each morphospecies were recorded.

Bee Preparation and Identification

All large bees, including *Bombus* specimens from which pollen was removed, were washed in soapy water, rinsed, and dried prior to pinning to prevent debris (pollen, oil, dirt) from obscuring key features. Pinned bees were labeled with locality, date of capture, and floral record data. Bees were sexed and identification was completed using the Discoverlife online interactive dichotomous keys, which allow for non-linear character specification of specimens. Identification of bee genera (and subgenera) was completed according to Michener and co-workers (1994) via Discoverlife.org, with reference to Packer and co-workers (2007). Andrenidae were identified to species using LaBerge (1985) and Mitchell (1960), Halictidae using Mitchell (1960), *Ceratina* using Rehan and Sheffield (2011), *Hylaeus* using Romankova (2007) and Mitchell (1960), Apidae using Mitchell (1962) (for *Bombus,* also Laverty and Harder (1988)), and Megachilidae using Sheffield and co-workers (2011) and Mitchell (1962). Bee determinations were confirmed with reference to collections held at the Nova Scotia Museum of Natural History and with help from Susan Westby. *Lasioglossum* were sorted to morphospecies, though a few specimens were identified to species using Gibbs and co-workers (2013) and Gibbs (2010, 2011). *Sphecodes* specimens (2 individuals) were assigned to a single morphospecies.

Data Analysis

Data analyses were performed using RStudio version 0.98.1102 (R Core Team 2014). Only data from days on which all site types received equal sampling effort were included in analyses of bee abundance, species richness, and community composition. Means and 95% confidence intervals were calculated for bee abundance and bee species richness in June (n = 2 sites, over 3 sampling days, for 3 site types) and August (n = 2 sites (except 1 urban ground level site), over 3 sampling days, for 3 site types). To assess bee inventory completeness and species richness across all site types, sample-based species accumulation curves (*n* = 2 sites, for 8 sampling days, for 3 site types) with estimated richness (100 runs without replacement) were generated using EstimateS 9.1.0 (Colwell 2005). Abundance and species richness of the three most common genera (*Andrena*, *Bombus*, and *Lasioglossum*) were compared among the three site types by calculating site type means and their corresponding 95% confidence intervals for June (*n* = 2 sites, over 3 sampling days, for 3 site types) and August (*n* = 2 sites (1 site for urban ground level), over 3 sampling days, for 3 site types).

Non-metric multidimensional scaling (NMDS) was performed to visualize variation in bee community composition across site types. Bee abundance data (from each site on each sampling day) was transformed using the Wisconsin double standardization technique; Bray-Curtis dissimilarity coefficients were generated from these data, with singletons removed (2 dimensions, stress = 0.16), and the bee communities were ordinated via NMDS using the vegan package in R (Oksanen et al. 2007). Plots of weighted averages were centered on the mean of the axes; ellipses representing 95% confidence regions were displayed for each site using the vegan and ggplot2 packages in R (Oksanen et al. 2007; Wickham 2009). To determine whether bee communities differed significantly ($\alpha = 0.05$) among sites, permutational multivariate non-parametric ANOVA (PERMANOVA) of differences (adonis function in the vegan package in R, 1000 permutations) was conducted on combined bee abundance data from both sampling periods. In addition, bee community similarity across sites was assessed via an analysis of similarities (ANOSIM; 999 permutations) conducted on Bray-Curtis dissimilarity indices generated from square-root transformed bee abundance data in PRIMER v.7 (Clarke & Gorley 2015; Clarke & Warwick 1994). Key bee species contributing to within-site similarity and between-site dissimilarity in bee communities were identified by calculating similarity percentages via SIMPER analysis in PRIMER.

To assess the attractiveness of focal flowers present within sampling plots at each site type, the proportion of visits to the focal species, *S. tridentata* and *S. bicolor,* was calculated for each day at each site according to the formula:

$$P_{target} = \frac{N_{Sibbaldiopsis} + N_{Solidago}}{N_{total}}$$

Where:

P_{target} = Proportion of bees captured on both focal species on a given day

$N_{Sibbaldiopsis}$ = Number of bees captured on *S. tridentata* per collection site on a given day

$N_{Solidago}$ = Number of bees captured on *S. bicolor* per collection site on a given day

N_{total} = Number of bees captured per collection site on a given day

Means and 95% confidence intervals were calculated to statistically compare daily focal flower attractiveness among site types. Linear regression was used to assess the relationship between visiting bee species richness and the number of flowering species visited at each site type.

To determine whether the pollen morphospecies richness of bumblebee-collected corbicular pollen loads differed significantly among the habitats studied, daily means for each site type (n = 2 green roofs for 3 days, n = 1 urban ground level site for 6 days, n = 2 coastal barrens for 3 days) and their corresponding 95% confidence intervals were calculated. To visualize whether different bumblebees species collected specific pollen morphotypes, pollen morphotype abundance data were ordinated via NMDS, with data treatment identical to that of the bee community NMDS procedure (2 dimensions, stress = 0.14). *Sedum* abundance (1 pollen load) was removed from the data set to relieve overplotting of all other pollen taxa. Statistical differences (α = 0.05) in pollen collection were determined by conducting a PERMANOVA (1000 permutations) on pollen morphotype abundance data, with bumblebee species and site included as factors. Plots of weighted averages were centered on the axes mean; ellipses representing 95% confidence regions were displayed for each bumblebee species and site type. In addition, pollen load compositional similarity across site types was assessed via ANOSIM (999 permutations) conducted on Bray-Curtis dissimilarity indices generated from square-root transformed pollen taxa abundance data in PRIMER. Identities of pollen taxa contributing to within-site type similarity and between-site type dissimilarity in bee-collected pollen loads were determined by calculating similarity percentages via SIMPER analysis in PRIMER.

Results

Wild bee communities

A total of 480 bees, comprising 54 species (including 8 *Lasioglossum,* 2 *Andrena,* and 1 *Sphecodes* morphospecies) and 12 genera, were collected across all sites and both collection periods; 204 bees were collected in June and 276 in August. An additional 50 bees were collected at green roof sites, increasing the total to 530, but were not included in analyses to ensure sampling effort was equal across sites and habitats (Table 8). The abundance of bees at coastal barrens sites (Mean ± SE), urban ground level sites, and green roof sites did not differ when sampling periods were pooled; however, distinct trends emerged when the two collection periods were considered separately. In June, daily capture rates did not differ among sites, with an average of 4.3 – 8.6 bees captured per sampling location per day; in August, bees were more abundant at coastal barrens sites (22.3 ± 2.8) relative to green roof sites (7.8 ± 1.3), while urban ground level sites displayed intermediate daily abundances (15.8 ± 3.8) (Figure 3).

Trends in daily mean bee species richness differed from those observed in bee abundance data. Urban ground level sites exhibited greater average daily bee species richness (6.3 ± 0.7) across sampling periods; green roof sites contained the least species rich samples (4 ± 0.2), and bee species richness at coastal barrens sites (5.8 ± 0.8) could not be differentiated from urban sites; richness trends were identical when June collections were examined independently, while no differences were detected in species richness among sites during the August collection period (Figure 3). Sample-based species accumulation curves indicated that sites differ in total species richness, with coastal barrens sites exhibiting a faster rate of species discovery and a greater final mean species count (33 ± 3.2) than green roof sites (20 ± 3.1) sampled; urban ground level sites displayed intermediate values (32 ± 4.1). Species accumulation curves failed to level off for all locations sampled (Figure 4).

Sites also displayed differences in daily mean bee richness at the generic level. More genera were captured per day at urban ground level sites (3.6 ± 0.5 genera) than green roof sites (2 ± 0.2) in June; coastal barrens sites could not be differentiated from urban locations on the basis of generic richness in June (2 ± 0.3). Conversely, coastal barrens sites displayed maximal mean daily bee generic richness values in July (4.7 ± 0.7); green roof samples contained fewer genera per day (2.3 ± 0.2) and an intermediate number of genera were captured per day at urban ground level sites (3.7 ± 0.5). The three most common genera collected across all site types were *Andrena*, *Bombus*, and

Lasioglossum (Figure 5). Other genera common to all site types included *Apis*, *Halictus*, *Hylaeus*, and *Megachile*. *Augochlorella* and *Ceratina* were only collected at ground level sites, occurring in both coastal barrens and the city. *Melissodes* and *Osmia* were collected only at coastal barrens sampling locations, while *Sphecodes* was only collected at an urban ground level site (Pine Hill). *Hylaeus affinis* (Smith) was collected in the Prospect barren, a new provincial record for this species.

Daily mean abundance and species richness of *Lasioglossum* bees did not differ among or within site types in June and August (Figures 6-7). *Andrena* abundances did not differ among site types within either collection period, but distinct trends were observed between sampling periods within each site type. On average, 2.3 andrenids (1.6 ± 0.5 species) were collected per day at coastal barrens sites and 0.7 andrenids (0.7 ± 0.3 species) per day at green roof sites in June, but no andrenids were recorded at either site type in August. Similarly, more andrenids were collected in June (2.2 ± 0.4 bees, 1.8 ±0.4 species) than August (0.3 ± 0.2 bees and species) per day at urban ground level sites. These trends were reversed in *Bombus* abundance and richness data. While within collection period abundance did not differ among site types, fewer bumblebees were caught per day at all sites in June (0.2 – 1.2 bees) compared to August (12.5 – 3.1 bees). While bumblebee species richness was similar across sites in June, more bumblebee species were collected per day at coastal barrens sites (3 ± 0.4) relative to green roof sites (1.2 ± 0.2) in August. Within site types, less species rich bumblebee samples were collected in June (0.2 – 0.8 species) compared to August (3 – 1.2 species). *Bombus terricola* was collected twice on the Atrium roof and once at the urban plot at Pine Hill but was not collected elsewhere.

PERMANOVA indicated that bee community composition differed significantly ($p = 0.001$) among the sites sampled based on species abundances (Figure 8). Similarly, analysis of similarity (ANOSIM) indicated that bee communities at individual sites did contain dissimilar constituent bee species ($p = 0.001$, $R = 0.35$). Similarity percentages indicated that the bee community with the greatest self-similarity (54.7% mean within-site sample similarity) occurred in the Herring Cove barrens; two urban locations, the Atrium green roof and Pine Hill ground level sites, displayed the lowest self-similarity (20.6 and 21.2, respectively), though two barrens locations, at Prospect and Chebucto Head, showed comparably low self-similarity (21.4 and 22.4, respectively).

Similarity percentages indicated that key species at each site frequently contributed to between site dissimilarity (Table 9). *Lasioglossum* morphospecies 2 provided the greatest source of community dissimilarity for the Atrium green roof relative to other sites. The Atrium bee community was not significantly different from those found in the Herring Cove barrens ($p = 0.13$, $R = 0.18$) or at the ground level urban site in Point Pleasant Park ($p = 0.19$, $R = 0.10$). The bee community present on the green roof at NSCC was differentiated from all other sites due to the abundance of *Lasioglossum* morphospecies 1. Within Point Pleasant Park, representing an urban ground level bee community, the greatest source of dissimilarity to other site types was contributed by *Lasioglossum* morphospecies 2 and *Andrena carlini*. The Pine Hill urban ground level site contained several species at abundances that increased dissimilarity to other sites, including *Lasioglossum* morphospecies 1 and 2, *Bombus ternarius*, *Bombus vagans*, and *Bombus impatiens*. At Chebucto Head, the bee species contributing the greatest dissimilarity to other sites was *B. vagans*. The bee community in the Chebucto Head barrens was similar to that present in the Herring Cove barrens ($p = 0.58$, $R = -0.11$), though Herring Cove contained greater mean abundances of shared bee species and was more species rich. The bee community in the Herring Cove barrens was primarily differentiated from other bee communities due to the abundance of *B. ternarius* and *Augochlorella aurata*; it did not appear distinct from the bee community sampled in the Prospect barrens ($p = 0.7$, $R = 0.45$). *Andrena carolina* was the primary driver of dissimilarity between the Prospect barrens bee community and those at all other sites.

Pollen loads

Floral communities at all sites contained both native and exotic co-flowering species (Tables 2-7). Across sites, flowering abundance trends were similar: few exotic species flowered May to mid-June (4.6 ± 0.7 species) while many flowered from mid-June to August (20 ± 2.6) and August – September (21 ± 2.9), though richness of native plant species in flower was similar across the entire summer (13.1 – 18 species) (Figure 9). Although pollen loads were only analyzed for bumblebees, floral visitation records indicate that, within sampling plots, the number of flowering species upon which bees were captured was positively correlated ($r^2 = 0.52$) with the species richness of bee visitors to a plot (Figure 10). Although the availability of receptive flowers for each target plant species (*S. tridentata* and *S. bicolor*) varied considerably among plots (627.6 ± 127.3 *S. tridentata* flowers, 24.3 ± 1.4 *S. bicolor* individuals in bloom), the proportion of bee captures on focal species did not differ significantly across site types (41 – 65% of bees captured) (Figure 11).

Thirty-seven unique pollen morphotypes were identified in 128 bumblebee pollen loads (Table 10). For each bumblebee, both the identity of the flower on which it was captured and the contents of its pollen load were characterized. The flower genera on which the most bumblebees were captured within sampling plots included *Solidago* (56), *Centaurea* (24), *Scorzoneroides* (12), *Campanula* (10), *Trifolium* (7), and *Rosa* (4). The frequency with which each plant species also occurred in a bee's pollen load varied; *Rosa* pollen appeared as the dominant grain type in 100% of the pollen loads collected by bees captured on *Rosa*. However, while *Centaurea* pollen occurred in 100% of the pollen loads of bees that were captured on *Centaurea*, only 45.7% of those pollen loads featured *Centaurea* as a dominant (> 100 grains) grain type. Of the most commonly contacted plant species, *Campanula* occurred the least frequently (40%) as a dominant grain in the pollen loads of bees that were captured on that species. The degree of pollen mixing by bumblebees differed among the three site types sampled in this study (Figure 12). Bumblebees captured at ground level sites in the coastal barrens (3.3 ± 0.2 pollen morphotypes) and city (3.8 ± 0.4) collected pollen from more plant taxa than bumblebees at green roof sites (1.9 ± 0.2).

The most common dominant (>100 grains) pollen type occurring in bumblebee pollen loads was *Solidago* (Table 10). Other common (occurring in >10% pollen loads) dominant grain types included *Spiraea, Taraxacum*-type (e.g. *Taraxacum*, *Scorzoneroides*, *Prenanthes*, *Hieracium*), *Centaurea*, *Trifolium*, and *Rubus*. Taxa that appeared as dominant grains in 10 – 5% of bee collected pollen loads included *Rosa*, *Hydrangea*, and *Mentha*-type. Of the remaining 22 morphotypes, 16 occurred as dominant grains in less than 5% of the bee collected pollen loads and 6 pollen morphotypes never exhibited counts greater than 25 grains.

The combination of pollen morphotypes constituting individual bumblebee pollen loads differed depending on the species of bumblebee collecting the pollen (ANOSIM: p = 0.004, R = 0.17; PERMANOVA: $p = 0.001$) and the sites at which pollen was collected (ANOSIM: p = 0.01, R = 0.18; PERMANOVA: $p = 0.001$). Across bumblebee species, *B. rufocinctus* demonstrated the lowest within-species pollen collection variability, with a mean pollen load similarity of 39.8% among *B. rufocinctus* foragers and a high abundance of *Campanula* and *Trifolium* pollen. Comparable levels of within-species similarity were displayed by *B. ternarius* (36.7%) and *B. vagans* (35.7%), both species favouring *Centaurea*, *Taraxacum*-type, and *Spiraea* pollen; and *B. impatiens* (34.8%), primarily collecting *Solidago* and *Taraxaum*-type pollen. *Hydrangea* pollen accounted for 100% of the within-species similarity of *B. bimaculatus,* the bumblebee species exhibiting the greatest within-species pollen load composition variability (10.1%).

Pollen load composition differed between *B. impatiens* and three other bumblebee species, *B. rufocinctus* ($p = 0.001$; $R = 0.59$; mean dissimilarity 91.7%), *B. vagans* ($p = 0.002$; $R = 0.42$; 81.6%), and *B. bimaculatus* ($p = 0.02$; $R = 0.41$; 83.9%) (Figure 13). Abundance of *Solidago* differentiated *B. impatiens* pollen loads from the *Campanula*-dominated loads of *B. rufocinctus* and the *Trifolium*-dominated loads of *B. vagans*. Collection of *Viburnum* pollen by *B. bimaculatus* contributed the most (13.62% dissimilarity contributed) to its separation from *B. impatiens* pollen load samples.

Bumblebees foraging at sites in different habitats appeared to focus on distinct pollen morphotypes during this study (Figure 14). Within-site similarity of bumblebee-collected pollen loads gathered at green roof sites (45.5% within-site similarity) were defined by abundance of *Solidago* (58.4%) and *Campanula* (20.4%). Bumblebees at urban ground level sites displayed the lowest within-site similarity (32.8%), driven by the contributions of *Solidago* (61.1%) and *Taraxacum*-type pollen (10.4%). *Centaurea* (44%), *Taraxacum*-type (22.7%), and *Spiraea* (14.8%) grains were the primary determinants of coastal barrens within-site similarity (36.6%). Pollen loads collected at green roof sites contained pollen taxa similar to ground level urban (67.3% similar) and coastal barrens sites (59.2% similar); however, pollen load compositions from coastal barrens sites differed significantly ($p = 0.029$, $R = 0.186$) from those collected at urban ground level sites (mean dissimilarity = 73.8%). At urban ground level sites, *Solidago* (11.2%), *Hypericum* (4.8%), and *Hydrangea* (4.6%) contributed to pollen load dissimilarity, while *Centaurea* (12.8%), *Taraxacum*-type (10.3%), *Trifolium* (10.1%), *Rubus* (5.3%), and *Rosa* (4%) represented the sources of greatest dissimilarity at coastal barrens sites.

Discussion

Bee abundance and richness

Bees frequently visited all habitats monitored in this study. Our observation of lower abundance and total richness in bee communities at green roof sites relative to those located in natural habitat must be interpreted cautiously due to low site type replication and fairly restricted sampling periods. However, these results correspond with findings from Tonietto and co-workers (2011), who compared bee communities on green roofs to those found in urban parks and natural prairie habitat in Chicago. Green roofs in Toronto also appeared to host less species rich and less abundant bee communities relative to ground level sites (Colla et al. 2009). In this study, the higher capture rates observed in August may reflect progressive increases in the colony size of certain social taxa (e.g. *Bombus, Halictus, Augochlorella*) that were more abundant at ground level locations.

The slope of species accumulation indicated that all sites sampled in this study, including green roofs, contained substantial undocumented bee richness. However, the absence of *Augochlorella* and *Ceratina* at green roof sites sampled is notable; these two genera were also absent from or found at very low abundances on green roofs in several other North American studies (Colla et al. 2009; Ksiazek et al. 2014; MacIvor et al. 2015; Tonietto et al. 2011). *Ceratina* nest in pithy stems (e.g. *Rubus*) (Packer et al. 2007), and lack of these nesting resources may dissuade these small bees from visiting green roofs. *Augochlorella* are eusocial, ground-nesting halictids, and foundresses produce workers, males, and queens over the course of the summer (Packer et al. 2007). As colonies increase in size, their resource requirements grow. Thus, the floral resources of a small green roof may not adequately support large, in situ colonies of *Augochlorella*, and, as with *Ceratina*, their small body size may prohibit continued visitation of green roofs for pollen or nectar. Furthermore, drought conditions, which occur frequently on green roofs, can reduce the productivity of *Augochlorella* colonies (Packer 1990), which may also reduce the likelihood of *Augochlorella* colony establishment on extensive green roofs.

In contrast to these genera, *Lasioglossum* commonly dominate green roof bee communities (Colla et al. 2009; Ksiazek et al. 2014; Tonietto et al. 2011), as found in this study. While *Lasioglossum* are abundant in the urban environment (Colla & Packer 2008; Fetridge et al. 2008; Matteson et al. 2008), their size precludes extended foraging flights (Greenleaf et al. 2007); Tonietto and co-workers (2011) suggested that these small sweat bees might nest directly on green roofs, with foragers relying entirely on green roof floral resources to provide both pollen and nectar. In contrast, MacIvor and co-workers (2015) found that bee communities on green roofs in Toronto featured more large and medium-bodied bees, such as *Bombus* and *Apis*; however, the roofs they sampled contained large populations of *Sedum*. To maximize pollen and nectar collection efficiency by reducing transitions between floral handling techniques (Heinrich 1979) and to capitalize on a locally abundant, florally homogeneous resource (Ishii 2006), bumblebees may have targeted synchronously flowering populations of *Sedum* on the Toronto green roofs. In contrast, the green roofs in this study featured low densities of mixed flowering species.

While the large body size and crop volume of bumblebees allow them to forage over long (>1 km) distances (Cresswell et al. 2000), increased body size also intensifies energy expenditure during flight (Heinrich 2004). It is unlikely that bumblebees would nest on extensive green roofs, as they prefer abandoned rodent burrows and tree cavities (Packer et al. 2007); therefore, each trip by a forager to a green roof involves energetic costs during vertical flight and foraging on the roof. Longer foraging distances have been shown to negatively affect bumblebee colony growth (Westphal et al. 2006), so sparse green roof floral resources or flowers with low nectar carbohydrate content (or volume) may create uneconomic foraging conditions for bumblebees when ground level resources are abundant. Nevertheless, even with differences in floral abundance among sites, the overall proportion of bees captured on our focal plant species within sampling plots was consistently high across site types, indicating that *S. tridentata* and *S. bicolor* are attractive floral resources for bees present in diverse habitats, including green roofs, in the Halifax Regional Municipality.

Green roofs likely place environmental filters on potential bee visitors, such as roof height (MacIvor 2015) and their associated energetic costs. Commonalities in green roof bee communities may reflect the small size of foraging patches present on green roofs, representing a resource pool of insufficient quality or quantity to overcome foraging costs associated with accessing these patches relative to more high quality or abundant resources proximal to the nest. Matteson and Langellotto (2010) found that urban bee richness was more influenced by urban garden area and sun exposure than surrounding green space cover, reinforcing the significance of floral patch size as a determinant of site attractiveness. Hence, green roofs may represent high quality habitat for small bees that nest directly on a green roof and low quality habitat for those that nest offsite. For large bees, the economics of visiting a green roof, and its associated habitat value, likely depend on ground level forage quality and abundance and the proximity of a green roof to the nest.

Bee community composition

Abundance and species richness are broad indicators of environmental productivity and diversity. However, the identities of bee species forming the bee fauna of a specific habitat help to assess relatedness of bee communities at different sites. Three of the most abundant bumblebees collected in this study, *B. impatiens*, *B. rufocinctus,* and *B. ternarius,* appear to be experiencing population increases in eastern North America. *B. vagans*, which was frequently found at ground level sites and which displayed a high abundance at barrens locations, appears to be in decline (Colla & Packer 2008). Two *B. terricola* were collected on the Atrium green roof, and another at the Pine Hill urban site. This bumblebee species is reported to be in decline in North America (Colla & Packer

2008) and was submitted in October 2015 for addition to the Species At Risk Act registry maintained by Environment and Climate Change Canada. It appears that some *B. terricola* were attracted to resources present within urban habitat in Halifax, and though none were collected during timed aerial netting, many *B. terricola* were observed foraging on *S. alba* and *C. nigra* in the Chebucto Head coastal barren. Andrenid presence at all sites in June and frequent visitation to *S. tridentata* on green roofs suggests that *S. tridentata* may represent attractive forage for these spring flying bees. Surveys of urban bees indicate that ground nesting *Andrena* are rare in the urban environment (Hernandez et al. 2009), so provision of attractive, early-blooming forage in the city, including on green roofs, may improve establishment of these highly effective pollinators (Javorek et al. 2002) in cities.

Pooled bee communities at green roof, urban ground level, and coastal barrens sites could not be differentiated, though distinct communities were observed at individual sites. The bee community on the NSCC green roof was distinct from all other sites sampled, while the Atrium green roof bee community was similar to the communities sampled at an urban park and a small coastal barren, due to the presence of *Lasioglossum* and *B. impatiens,* respectively. Both shared taxa represent highly abundant urban-adapted bees (Fetridge et al. 2008; Matteson et al. 2008; Packer et al. 2007; Colla & Packer 2008). The distinctive community on the NSCC green roof was defined by the presence of a different *Lasioglossum* morphospecies. The appearance of abundant but distinct *Lasioglossum* morphospecies on both green roofs suggests, as in other studies (Colla et al. 2009; Tonietto et al. 2011) that members of this genus are well adapted to the green roof environment, but also suggests that the character of surrounding green space may influence which species visit green roofs (Braaker et al. 2013), though area of surrounding green space was not measured here.

The urban residential site at Pine Hill contained a diverse bee community, including a parasitic genus, *Sphecodes*, which was not collected at any other site. As a parasite of other halictids (Packer et al. 2007), *Sphecodes* at this site were likely targeting abundant *H. rubicundus.* Similar to the Atrium green roof, correspondence between the urban bee community at Pine Hill and that in the Herring Cove barren centered on similarities in *B. impatiens* abundance. The Pine Hill site contained shrubs (e.g. *Morella, Ilex, Aronia, Vaccinium*) common to the Herring Cove barren but sparse elsewhere in the city. *Osmia simillima,* a cavity-nesting bee, was not found at the urban Pine Hill location but was present at Herring Cove. Proximity to a forest edge provided much woody debris at Herring Cove, with many logs exhibiting signs of beetle activity. These features would contribute nesting sites for cavity-nesting *Osmia* at Herring Cove (Packer et al. 2007). As the area planted with native species increases in urban gardens, abundance of native bees, especially bumblebees, appears to also increase (Fukase & Simons, 2016). The residential yard sampled at Pine Hill features an atypical diversity of native plants relative to neighbouring properties, which may attract urban bumblebees like *B. impatiens.*

Among the barrens, Chebucto Head and Herring Cove featured similar bee communities, with both sites hosting similar abundances of *B. vagans.* However, Herring Cove was more species rich than Chebucto Head. Proximity to a forest edge has been shown to increase bee richness in blueberry fields (Cutler et al. 2015; Moisan-DeSerres et al. 2014), and the forested boundary of the Herring Cove barren may produce greater environmental heterogeneity, and thus nesting opportunities, at that site relative to the other, more extensive barrens sampled. The bee community present in the Prospect barren was distinct from all sites except the community in the Herring Cove barren, with which it shared a large population of *B. vagans*. The andrenid *A. carolina*, collected in abundance at Prospect, was absent at all other sites. *A. carolina* specializes on Ericaceae, and work by Tuell and co-workers (2009) indicated that *A. carolina* collected pollen exclusively from *Vaccinium* when lowbush blueberry was in bloom. Barrens are characterized by predominantly ericaceous, shrubby plant communities and *Vaccinium* was present at all barrens sites sampled in this study; thus, certain coastal barrens may represent high quality habitat for this species. Sellars and Hicks (2015) also found *A. carolina* to be highly abundant in open woodland in Newfoundland. One male *Hylaeus affinis* (Smith) was collected in the coastal barrens at Prospect, representing a new provincial record for this species. Together, undocumented species richness, indicated by species accumulation curves, presence of *Vaccinium* specialists, and a new provincial record of *H. affinis* suggest that further sampling of bee communities in coastal barrens environments is warranted.

Pollen load composition

Increasingly diverse bee communities appeared to visit more diverse flowering species in sampling plots studied here, consistent with the findings of Potts and co-workers (2003). However, visitation patterns alone may not adequately characterize the dietary importance of pollen sources: significant variability was exhibited in the dominance of pollen grains collected from plant species on which bumblebee capture occurred. Accordingly, pollen load analysis is likely to yield a more accurate and descriptive account of bumblebee pollen foraging history and preference. However, nectar is the primary energy currency of adult foraging bees, so visits to flowers that do not result in pollen dominance might also indicate that foragers were drinking nectar without collecting pollen. Within the broader foraging context surrounding our sampling plots, richness of native plants available as sources of nectar and pollen was constant across the summer, whereas the availability of exotic floral resources increased dramatically by mid-summer. Pollen load analysis revealed that bumblebees in urban and coastal barrens environments capitalized on both native and non-native pollen. Bumblebee foraging fidelity was lower in urban ground level and coastal barrens environments relative to green roofs. None of the ground level sites featured large monocultures of any flowering species, though green roofs contained the fewest species – with only *Solidago* and *Campanula* in bloom in large quantities. This may explain the greater pollen collection constancy observed on green roofs relative to ground level sites.

Few bumblebee species displayed distinct pollen load compositions – though *B. impatiens* collected pollen loads that differed from three bumblebee species. *B. impatiens* showed a preference for *Solidago* pollen, whereas the other bee species collected pollen from more diverse sources. In particular, *B. rufocinctus* appeared to target *Campanula rotundifolia* flowers present on the NSCC green roof. The relative lack of distinction among pollen loads collected by bumblebee species accords with their role as generalist foragers and agrees with the findings of Jha and Kremen (2013).

In Halifax, *Solidago* appeared to be an important source of pollen for bumblebees, especially in the urban environment. The pollen loads collected by bumblebees on green roofs were similar to those collected at our urban ground level and coastal barrens sites. However, bumblebees collected distinct pollen loads at coastal barrens sites relative to urban ground level sites. Though bumblebees at both locations relied on native pollen sources, like *Spiraea,* and exotic pollen sources, like *Hieracium* or *Scorzoneroides*, bumblebees at urban ground level sites collected more pollen from *Solidago*, while coastal barrens foragers collected *Centaurea* and *Trifolium* pollen and relied less on *Solidago.* Both *Solidago* and *Spiraea* are known to be attractive to pollinators despite minimal nectar rewards due to their ease of handling, as bees can crawl across inflorescences and contact multiple flowers with minimal energy expenditure (Harder 1990; Heinrich 1975; Robson 2008; Werner et al. 1980). For bumblebees, pollen handling requires more time to learn than does nectar handling (Raine & Chittka 2006), which may explain the high frequency of *Solidago* grains in bee pollen loads despite low nectar reward. The protein-rich pollen offered by *Trifolium* (Hanley et al. 2008) frequently attracts bumblebees foraging in urban environments (Larson et al. 2014). In Britain where it is native, *Centaurea nigra* is a highly valuable forage resource for bumblebees (Carvell et al. 2006).

As generalists, bumblebees may benefit from the added floral resources offered by exotic plant species (Jha et al. 2013). Hinners and Hjelmroos-koski (2009) found that bees collected large amounts (45%) of exotic pollen taxa in urban grasslands, and in disturbed habitat, bees foraged on exotic plant species when availability of native flowers was limited (Williams et al. 2011). However, a high frequency of pollen collection from exotic species has the potential to reduce bumblebee interactions with native barrens plant species. Grass and co-workers (2013) reported that an increase in abundance of exotic plants promoted generalist pollinators and generalist pollination strategies. Several studies have indicated that coastal barrens communities host rare plant species and plant communities differing from other environments in Nova Scotia (Cameron & Bondrup-Nielsen 2013; Oberndorfer & Lundholm 2009; Porter 2013). The relationships between rare plants and their pollinators in Nova Scotia coastal barrens remain poorly understood. Bee-pollinated plant species with patchy, low-density distributions (e.g. *Agalinis, Saxifraga, Silene*) may be vulnerable to pollen limitation if these plants must compete for pollinators with large aggregations of highly attractive exotics (Geslin et al. 2014). Understanding the impact of exotic invaders on plant-pollinator relationships in coastal barrens in Nova Scotia could benefit efforts to conserve some rare plant species.

Conclusion

The ecosystem services provided by green roofs to city dwellers have steadily increased their popularity. In the last decade, research has begun to examine the potential for these features to provide suitable habitat for plants and animals. Multiple studies have established that invertebrates, including bees, visit green roofs and these findings have prompted claims of green roof habitat provisioning for urban invertebrates. Without a direct linkage between faunal associates and green roof resources, these claims could not be substantiated. Results from this study indicate that native-planted green roofs can serve as habitat for a number of urban bee taxa; however, the suitability of green roof habitat depends on the species of bee. Our findings also demonstrated that some native-planted green roofs can host bee communities similar to those found at ground level and coastal barrens sites, though further sampling at additional sites and for a greater portion of the summer is needed to confirm these patterns. Common, urban-adapted species linked roof communities to urban ground level and proximal coastal barrens sites; however, larger, more geographically distant coastal barrens did not host bee communities similar to native planted green roofs. Despite differences in bumblebee pollen collection habits between urban ground level and coastal barrens sites detected in this study, bumblebees on native-planted green roofs showed pollen collection habits intermediate between the two ground level environments – indicating that foraging options on our native-planted green roofs diversified the pollen taxa available to and used by urban bees in Halifax. Two native plant species, *S. tridentata* and *S. bicolor* appeared to represent attractive forage options for bee species, with *S. bicolor* contributing significantly to the pollen load content of bumblebee foragers. However, abundant exotic plant species can also provide pollen resources to wild bee foragers in urban and natural environments. Strategic species selection, along with increased diversity and abundance of floral resources on green roofs may improve their suitability for a wider range of bee taxa, while a better understanding of nest provisioning may explain the absence of some taxa. Further research on green roof habitat usage patterns by bees of different body sizes in response to differential forage patch size and quality could improve the habitat value of green roofs for urban bees.

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Tables

Table 1. Bee collection locations by site type and focal plant species bloom time.

		Site Types		
Focal species	Green roof	Urban ground	Coastal barrens	Period
S. tridentata	Atrium, NSCC	Pine Hill, Point Pleasant	Chebucto Head, Herring Cove	June 23 – July 2
S. bicolor	Atrium, NSCC	Pine Hill N/A	Chebucto Head, Prospect	August 5 – 12

Table 2. Native plant species in bloom from May to mid-June by site type. Presence of "**x**" indicates observation of >5 individuals within 250 m of sampling plots at that site.

May to mid-June							
	Green roof		**Urban ground level**		**Coastal barrens**		
Native Genus	Atrium	NSCC	Pine Hill	Point Pleasant	Chebucto Head	Prospect	Herring Cove
Acer	**x**	**x**	**x**	**x**	**x**		**x**
Alnus				**x**	**x**	**x**	**x**
Amelanchier	**x**			**x**	**x**	**x**	**x**
Aralia				**x**	**x**	**x**	**x**
Arctostaphylos					**x**	**x**	
Arethusa					**x**	**x**	
Argentina						**x**	
Aronia			**x**		**x**	**x**	**x**
Chamaedaphne					**x**	**x**	
Clintonia				**x**			
Convallaria				**x**			
Corema					**x**	**x**	
Cornus	**x**		**x**	**x**	**x**	**x**	**x**
Empetrum			**x**		**x**	**x**	**x**
Epigaea				**x**			**x**
Fragaria	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Gaylussacia					**x**	**x**	**x**
Houstonia	**x**	**x**		**x**			
Hudsonia	**x**				**x**		
Ilex			**x**		**x**	**x**	**x**
Ledum					**x**	**x**	
Lonicera						**x**	
Maianthemum	**x**			**x**	**x**	**x**	**x**
Morella		**x**	**x**	**x**	**x**	**x**	**x**
Prunus					**x**		
Salix			**x**		**x**		
Rhodiola	**x**	**x**	**x**		**x**	**x**	
Rhododendron			**x**		**x**	**x**	
Sarracenia					**x**	**x**	
Trientalis				**x**	**x**	**x**	**x**
Vaccinium			**x**	**x**	**x**	**x**	**x**
Total	8	5	11	14	25	23	15

Table 3 Exotic plant species in bloom from May to mid-June. Presence of "**x**" indicates observation of >5 individuals within 250 m of sampling plots at that site.

May to mid-June							
	Green roof		**Urban ground level**		**Coastal barrens**		
Exotic Genus	Atrium	NSCC	Pine Hill	Point Pleasant	Chebucto Head	Prospect	Herring Cove
Aesculus				**x**			
Aquilegia	**x**						
Cerastium	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Ilex	**x**						
Malus	**x**		**x**				
Magnolia	**x**						
Oxalis	**x**	**x**	**x**	**x**			**x**
Ranunculus	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Tussilago	**x**	**x**	**x**	**x**	**x**		**x**
Typha		**x**					
Total	8	5	5	5	3	2	4

Table 4. Native plant species in bloom from mid-June to August. Presence of “**x**” indicates observation of >5 individuals within 250 m of sampling plots at that site.

	mid-June to August						
	Green roof		**Urban ground level**		**Coastal barrens**		
Native Genus	Atrium	NSCC	Pine Hill	Point Pleasant	Chebucto Head	Prospect	Herring Cove
Achillea	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Angelica						**x**	**x**
Argentina						**x**	
Aronia			**x**	**x**	**x**	**x**	**x**
Campanula	**x**	**x**	**x**		**x**	**x**	**x**
Cornus	**x**		**x**	**x**	**x**	**x**	**x**
Cypripedium							**x**
Diervilla			**x**	**x**	**x**		
Erigeron	**x**	**x**	**x**				
Euphrasia					**x**		**x**
Fragaria	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Galium	**x**	**x**					
Gaultheria				**x**	**x**	**x**	**x**
Hudsonia	**x**				**x**		
Ilex			**x**		**x**	**x**	**x**
Iris		**x**				**x**	**x**
Kalmia				**x**	**x**	**x**	
Lathyrus				**x**		**x**	**x**
Mitchella				**x**			
Plantago	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Potentilla		**x**	**x**	**x**	**x**		**x**
Prunella	**x**	**x**	**x**	**x**			
Rhodiola	**x**	**x**	**x**		**x**	**x**	
Rhus				**x**	**x**		
Rubus		**x**	**x**	**x**	**x**	**x**	**x**
Sarracenia					**x**	**x**	
Sibbaldiopsis	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Sisyrinchium			**x**		**x**	**x**	**x**
Sorbus					**x**	**x**	**x**
Trientalis				**x**	**x**	**x**	**x**
Vaccinium			**x**	**x**	**x**	**x**	**x**
Viburnum	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Total	12	13	17	18	23	22	21

Table 5. Exotic plant species in bloom from mid-June to August. Presence of "**x**" indicates observation of >5 individuals within 250 m of sampling plots at that site.

mid-June to August							
	Green roof		**Urban ground level**		**Coastal barrens**		
Exotic Genus	Atrium	NSCC	Pine Hill	Point Pleasant	Chebucto Head	Prospect	Herring Cove
Allium	**x**	**x**			**x**		
Cerastium	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Daucus	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Epilobium	**x**	**x**					
Erysimum		**x**					
Glechoma						**x**	
Hemerocallis	**x**	**x**	**x**				
Hieracium	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Hosta	**x**	**x**	**x**				
Hypericum		**x**	**x**	**x**	**x**		
Ilex	**x**						
Impatiens		**x**					
Leontodon		**x**		**x**	**x**		**x**
Leucanthemum		**x**	**x**	**x**			
Liatris			**x**				
Linaria				**x**			
Lotus		**x**					
Lupinus		**x**			**x**		**x**
Malva		**x**					
Matricaria		**x**	**x**	**x**			**x**
Medicago	**x**	**x**	**x**	**x**	**x**		
Melilotus		**x**	**x**				
Oxalis	**x**	**x**	**x**	**x**			**x**
Paeonia			**x**				
Plantago	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Polygonum	**x**	**x**		**x**		**x**	
Ranunculus	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Raphanus		**x**					**x**
Rhinanthus					**x**	**x**	
Rorippa	**x**						
Sagina	**x**						

Sedum	x	x	x				
Senecio	x	x	x	x			
Solanum			x	x			
Sorbus			x	x			
Stellaria	x	x	x	x	x	x	x
Taraxacum	x	x	x	x	x	x	x
Thymus			x				
Trifolium	x	x	x	x	x	x	x
Veronica	x	x	x	x			
Viburnum		x					
Vicia	x	x	x	x	x	x	x
Total	22	31	25	21	15	12	14

Table 6. Native plant species in bloom from August to September. Presence of "**x**" indicates observation of >5 individuals within 250 m of sampling plots at that site.

	August to September						
	Green roof		**Urban ground level**		**Coastal barrens**		
Native Genus	Atrium	NSCC	Pine Hill	Point Pleasant	Chebucto Head	Prospect	Herring Cove
Achillea	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Anaphalis	**x**			**x**	**x**		
Campanula	**x**	**x**	**x**		**x**	**x**	**x**
Conyza	**x**	**x**					
Doellingeria				**x**	**x**	**x**	**x**
Erigeron	**x**	**x**		**x**			
Euphrasia					**x**		
Euthamia			**x**	**x**	**x**	**x**	**x**
Gaultheria				**x**	**x**	**x**	**x**
Oclemena					**x**		
Oenothera		**x**		**x**	**x**		
Plantago	**x**	**x**		**x**	**x**	**x**	**x**
Prenanthes				**x**	**x**	**x**	**x**
Prunella	**x**	**x**	**x**	**x**	**x**		
Rosa			**x**	**x**	**x**	**x**	**x**
Rubus		**x**	**x**	**x**	**x**	**x**	**x**
Sibbaldiopsis	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Solidago	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Spiraea			**x**	**x**	**x**	**x**	**x**
Symphyotrichum	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Thalictrum						**x**	
Total	10	11	10	16	18	14	13

Table 7. Exotic plant species in bloom from August to September. Presence of "**x**" indicates observation of >5 individuals within 250 m of sampling plots at that site.

	August - September						
	Green roof		**Urban ground level**		**Coastal barrens**		
Exotic Genus	Atrium	NSCC	Pine Hill	Point Pleasant	Chebucto Head	Prospect	Herring Cove
Allium		**x**		**x**	**x**		
Bidens			**x**	**x**			
Centaurea		**x**		**x**	**x**		**x**
Cerastium	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Daucus	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Epilobium	**x**	**x**					
Hemerocallis	**x**	**x**	**x**				
Hieracium	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Hosta	**x**	**x**	**x**				
Hydrangea	**x**		**x**				
Hypericum		**x**	**x**	**x**	**x**		
Impatiens		**x**					
Leontodon	**x**	**x**		**x**	**x**	**x**	**x**
Leucanthemum		**x**	**x**	**x**	**x**		
Linaria				**x**			
Lotus		**x**					
Lupinus		**x**			**x**		**x**
Matricaria	**x**	**x**	**x**	**x**			**x**
Medicago	**x**	**x**	**x**	**x**	**x**		
Melilotus		**x**	**x**				
Oxalis	**x**	**x**	**x**	**x**			**x**
Plantago	**x**	**x**	**x**	**x**	**x**		**x**
Polygonum	**x**	**x**				**x**	
Ranunculus	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Raphanus		**x**					**x**
Rhinanthus					**x**	**x**	
Rudbeckia		**x**					
Sagina	**x**						
Sedum	**x**	**x**	**x**				
Senecio	**x**	**x**	**x**	**x**	**x**		
Solanum			**x**	**x**			
Sonchus		**x**	**x**		**x**		**x**
Spiraea	**x**	**x**	**x**				
Stellaria	**x**	**x**	**x**	**x**	**x**	**x**	**x**

Tanacetum	**x**						
Taraxacum	**x**	**x**	**x**	**x**	**x**		**x**
Thymus			**x**				
Trifolium	**x**	**x**	**x**	**x**	**x**		**x**
Veronica	**x**	**x**	**x**	**x**			
Vicia	**x**	**x**	**x**	**x**	**x**		**x**
Total	24	32	26	22	19	8	16

Table 8. Identity of bees collected from each site type across sampling periods. Presence of "**x**" indicates collection of at least one individual within that site type.

Family	Genus	Species	Green Roof	Urban Ground	Barrens
Andrenidae	*Andrena*	*algida*		x	x
		carlini		x	x
		carolina			x
		ceanothi	x		x
		crataegi	x	x	x
		mandibularis			x
		milwaukeensis	x	x	x
		miranda		x	
		nigrihirta			x
		nivalis	x	x	x
		regularis	x	x	x
		wilkella	x	x	
		w-scripta	x	x	x
		morphospecies1		x	
		morphospecies2		x	
Apidae	*Apis*	*mellifera*	x	x	x
	Bombus	*bimaculatus*	x	x	x
		citrinus			x
		fernaldae		x	x
		impatiens	x	x	x
		insularis			x
		rufocinctus	x		
		sandersoni		x	
		ternarius		x	x
		terricola	x	x	
		vagans		x	x
	Ceratina	*calcarata*		x	
		mikmaqi			x
	Melissodes	*illata*			x
Colletidae	*Hylaeus*	*affinis*			x
		mesillae	x	x	
		modestus			x
Halictidae	*Augochlorella*	*aurata*		x	x
	Halictus	*confusus*		x	
		ligatus	x		
		rubicundus	x	x	x
	Lasioglossum	*coriaceum*		x	
		cressonii	x	x	x

		tegulare		x	
		morphospecies1	x	x	x
		morphospecies2	x	x	x
		morphospecies3	x	x	x
		morphospecies4	x		
		morphospecies5	x	x	
		morphospecies6	x	x	
		morphospecies7			x
		morphospecies8			x
	Sphecodes	morphospecies1		x	
Megachilidae	*Megachile*	*frigida*	x		
		inermis			x
		melanophaea	x	x	x
		montivaga			x
		relativa/lapponica			x
	Osmia	*simillima*			x

Table 9. Dissimilarity percentages for bee species contributing to greatest site dissimilarity (per comparator site) between site pairs.

Comparator Site 1	Comparator Site 2	Dis. Sp. 1	Contrib. Dis. (%)	Dis. Sp. 2	Contrib. Dis. (%)	Mean Dis. (%)
Atrium	Chebucto Head	*Las. 2*	11.3	*B. vagans*	15.94	92.8
Atrium	Herring Cove	*Las. 2*	5.8	*B. ternarius*	13.2	84.5
Chebucto Head	Herring Cove	None[1]	N/A	*A. aurata*	11.01	72.9
Atrium	NSCC	*Las. 2*	15.3	*Las. 1*	17.65	85.3
Chebucto Head	NSCC	*B. vagans*	17.8	*Las. 1*	14.15	91.4
Herring Cove	NSCC	*B. ternarius*	13.4	None[1]	N/A	87.5
Atrium	Pine Hill	*Las. 2*	10.5	*B. impatiens*	14.4	85.1
Chebucto Head	Pine Hill	*B. vagans*	12	*B. impatiens*	12.51	87.6
Herring Cove	Pine Hill	*B. ternarius*	10.8	*A. aurata*	9.61	80.8
NSCC	Pine Hill	*Las. 1*	12.3	*B. impatiens*	15.08	85.9
Atrium	Point Pleasant	*Las. 1*	11.9	*Las. 2*	13.23	80.4
Chebucto Head	Point Pleasant	*B. vagans*	15.4	*Las. 2*	10.43	90.8
Herring Cove	Point Pleasant	*B. ternarius*	13.7	*Las. 2*	5.72	77
NSCC	Point Pleasant	*Las. 1*	13.2	*Las. 2*	13.31	87
Pine Hill	Point Pleasant	*B. impatiens*	12.8	*Las. 2*	9.57	85.4
Atrium	Prospect	*Las. 2*	14.4	*A. carolina*	15.21	90.1
Chebucto Head	Prospect	*B. vagans*	17.2	*A. carolina*	13.25	91.6
Herring Cove	Prospect	*A. aurata*	11	*A. carolina*	6.71	89.9
NSCC	Prospect	*Las. 1*	19.2	*A. carolina*	15.65	99.5
Pine Hill	Prospect	*B. impatiens*	14.4	*A. carolina*	11.22	96
Point Pleasant	Prospect	*A. carlini*	14.3	*A. carolina*	15.03	88

Note: [1] Site did not contain any key species with greater abundance than the comparator site.

Table 10. . Pollen taxa identities and grain dominance frequency in August-collected bumblebee pollen loads.

	Frequency		
Pollen morphotype	**10-49 grains**	**50-99 grains**	**100+ grains**
Achillea	2	1	1
Borago	1	1	1
Campanula	9	7	5
Centaurea	65	43	29
Cerastium	1	1	1
Chamerion	1	1	1
Cirsium	4	0	0
Daucus	8	2	1
Diervilla	1	0	0
Ericaceae-type	1	1	1
Erigeron	2	1	1
Euphrasia	1	1	1
Galium	1	0	0
Gaultheria	11	6	4
Hosta	9	2	2
Hydrangea	13	10	10
Hypericum	4	2	2
Impatiens	2	1	1
Liliaceae-type	1	1	1
Mentha-type	11	9	7
Onagraceae-type	1	0	0
Plantago	2	2	2
Prunella	1	1	1
Rosa	17	14	12
Rubus	14	13	13
Sedum	2	1	1
Sibbaldiopsis	2	2	2
Solanum	4	3	3
Solidago	68	54	40
Spiraea	45	38	34
Taraxacum-type	60	38	30
Trifolium	37	29	27
Urtica-type	1	1	1
Viburnum	12	5	5
Vicia	4	1	1
Unknown1	1	0	0
Unknown2	1	0	0

Figures

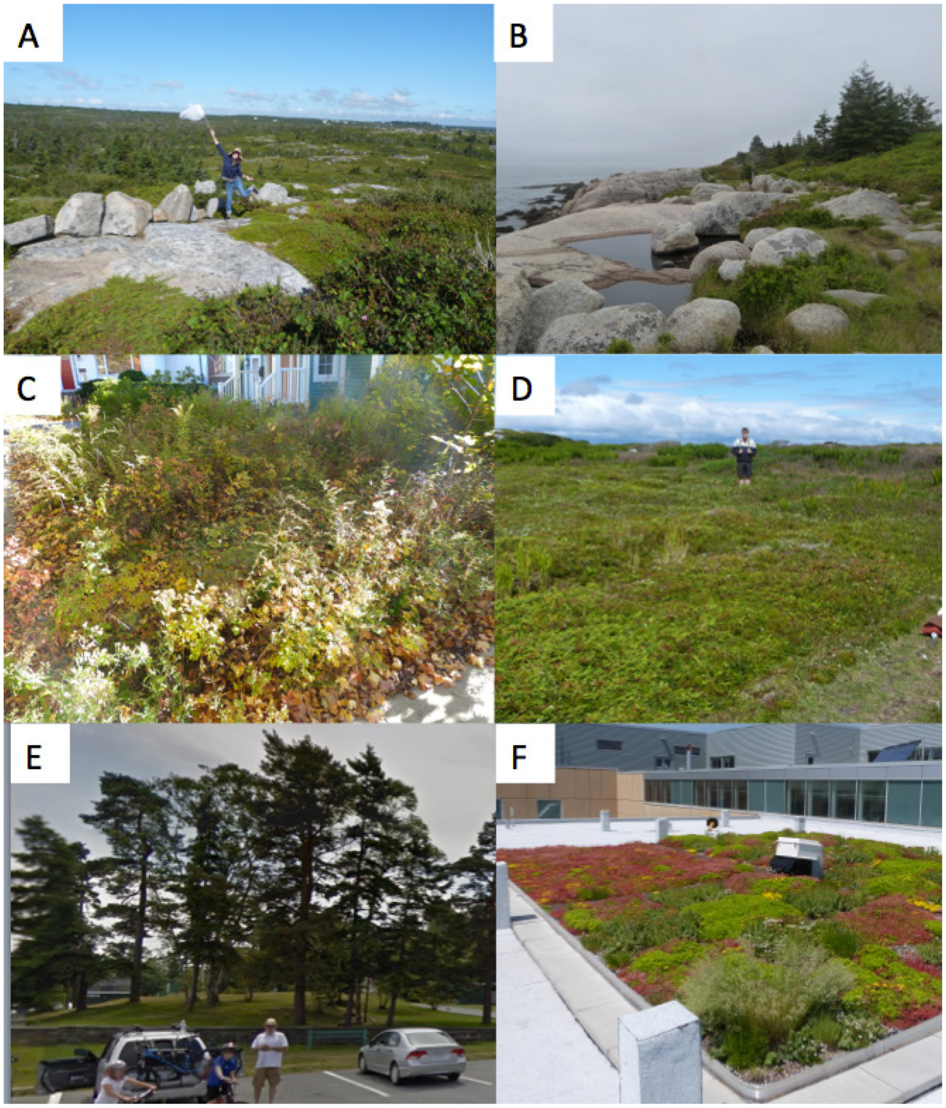

Figure 1. Photos of bee collection sites. A: Chebucto Head B. Herring Cove C. Pine Hill D. Prospect E. Point Pleasant Park. F. NSCC green roof. Photo E sourced from Google Maps street view. Photo of Atrium green roof available in Chapter 2 (Figure 1).

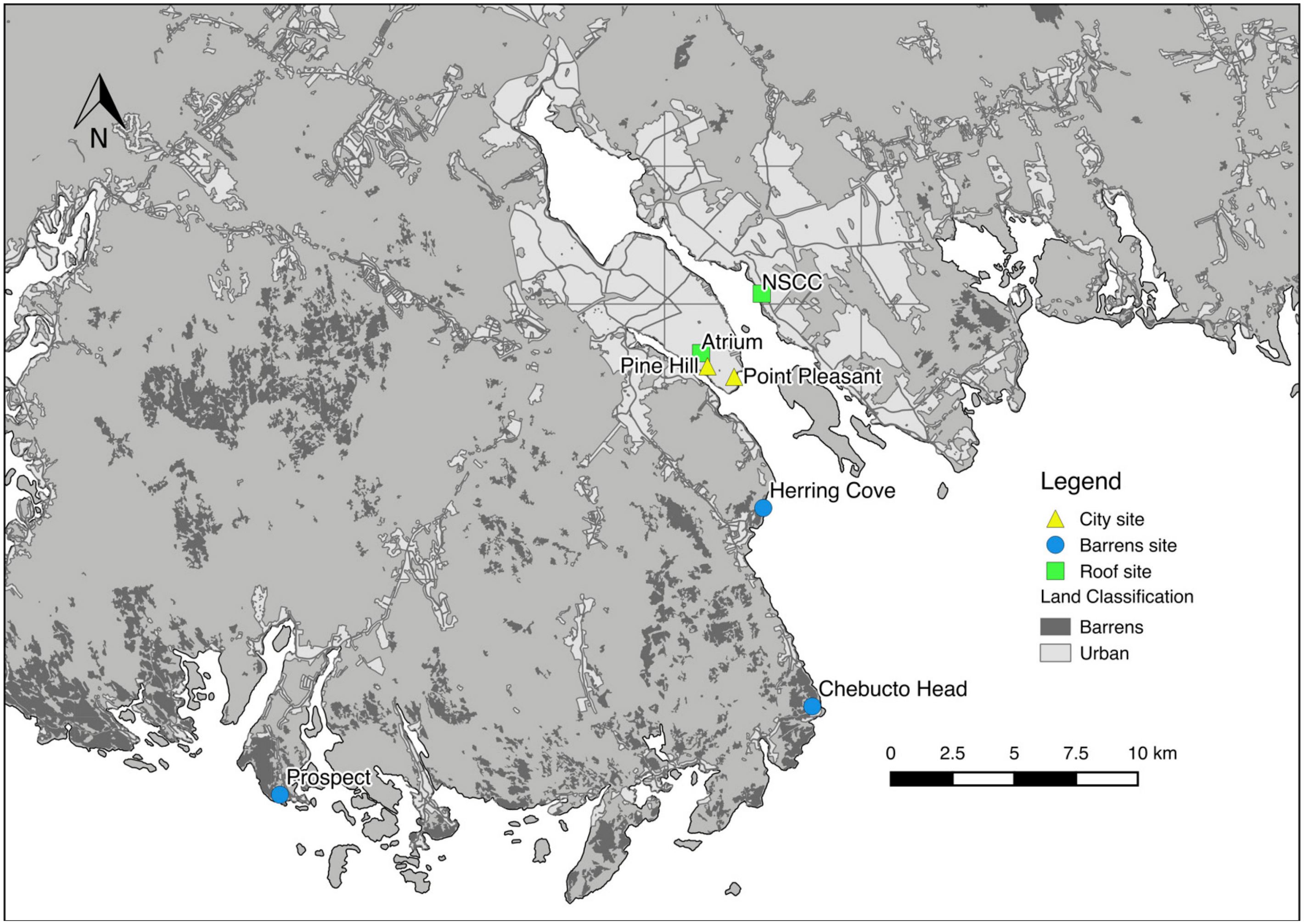

Figure 2. Map of bee collection locations and land use classification in Halifax county; land use data from NS DNR (2015), base map from Hijmans and co-workers (2015).

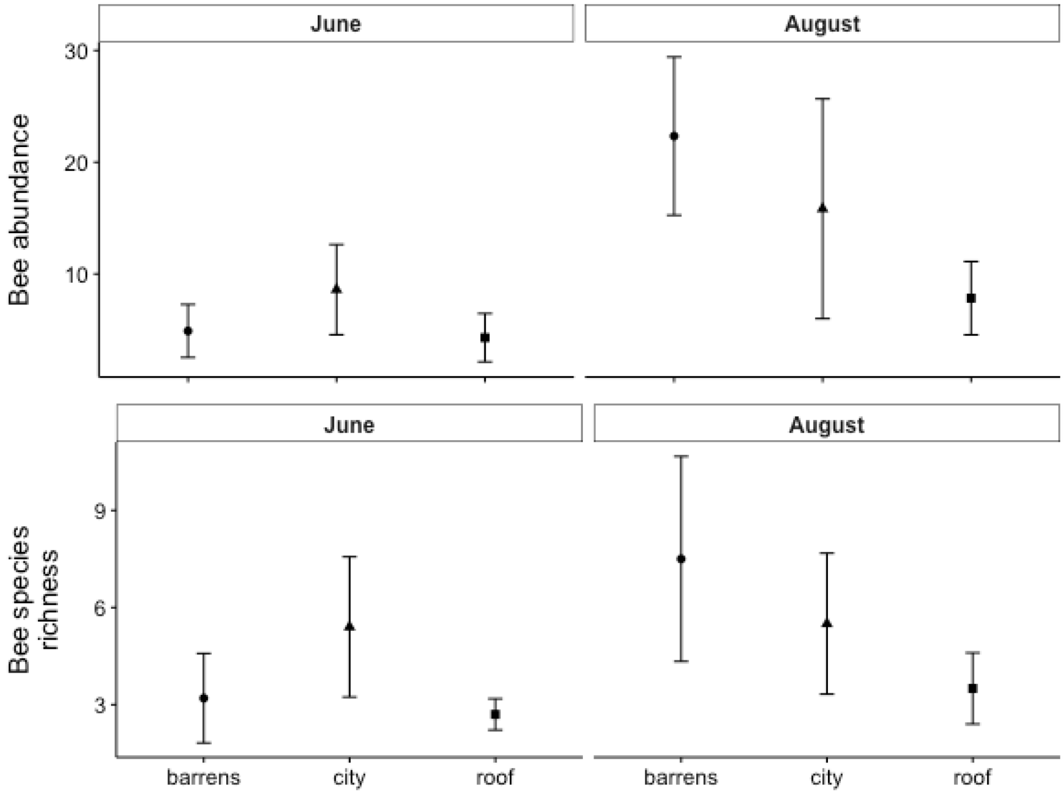

Figure 3. Mean daily bee abundance and species richness by site type in June (*n* = 2 sites, over 3 sampling days, for 3 site types) and August (*n* = 2 sites (1 site at urban ground level), over 3 sampling days, for 3 site types). Bars represent 95% confidence intervals.

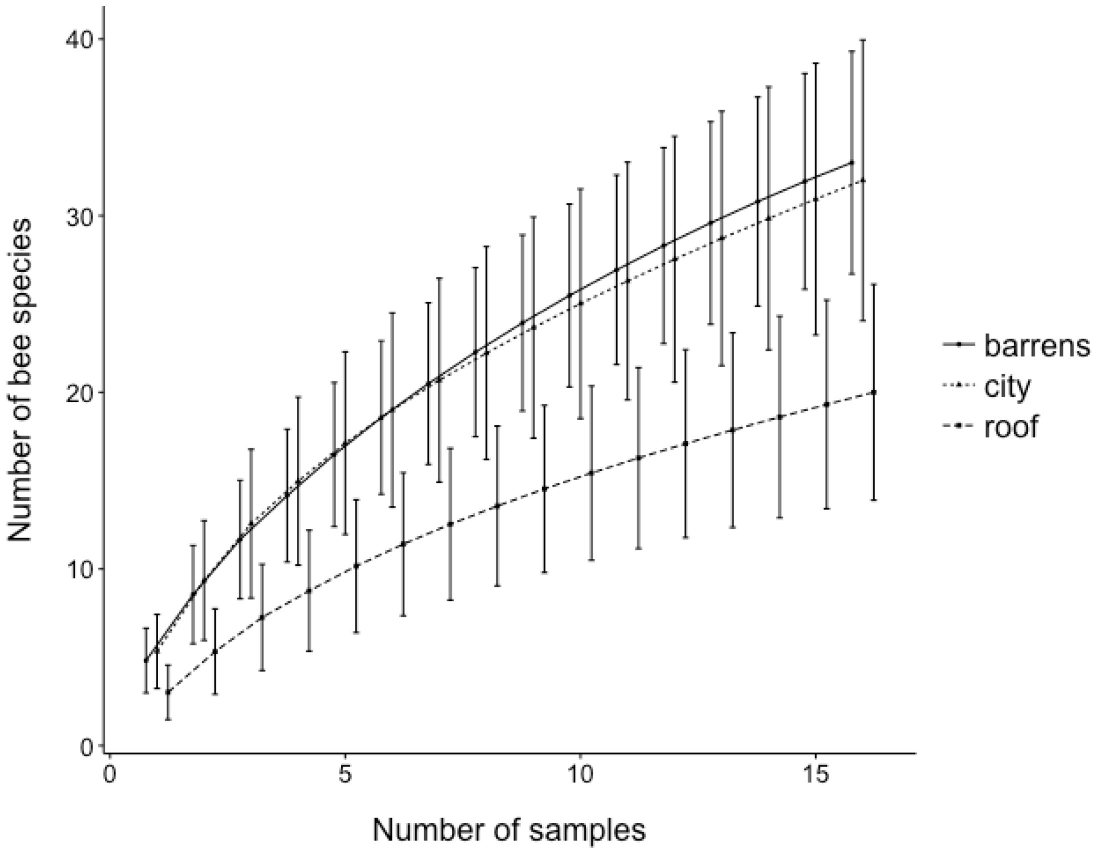

Figure 4. Sample-based species accumulation curves generated for each site type (*n* = 2 sites, over 8 sampling days, for 3 site types) across sampling periods. Richness estimates were generated using EstimateS v.9.1.0 (Colwell 2005). Bars represent 95% confidence intervals.

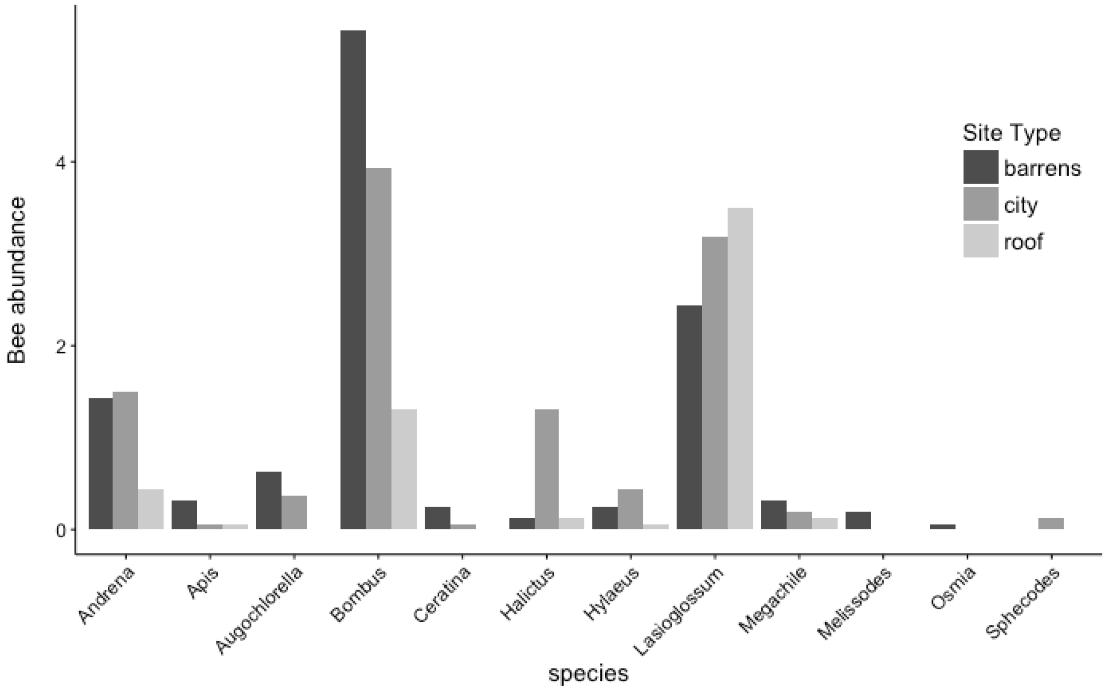

Figure 5. Mean daily abundance of bee genera at each site type (June: *n* = 2 sites, over 3 sampling days, for 3 site types; August: *n* = 2 sites (1 site for urban ground level), over 3 sampling days, for 3 site types).

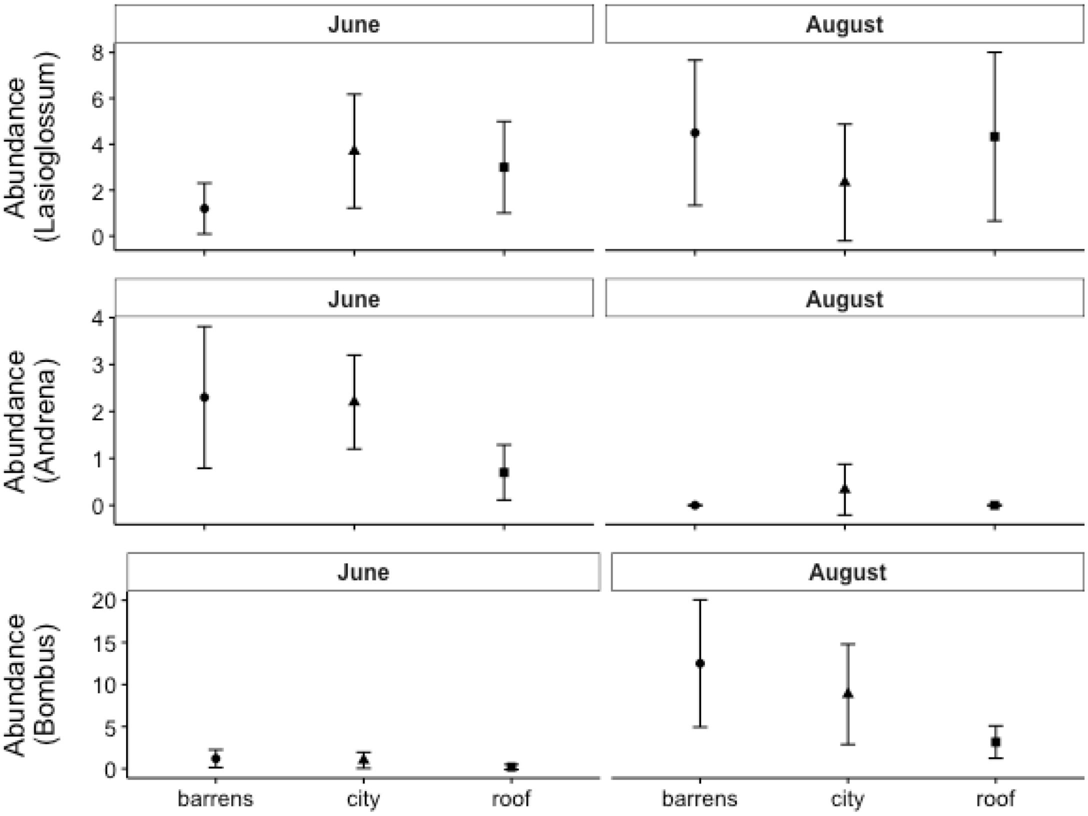

Figure 6. Average daily abundance of the three most common genera (*Lasioglossum*, *Andrena*, and *Bombus*) collected at all sampling locations in June (*n* = 2 sites, over 3 sampling days, for 3 site types) and August (*n* = 2 sites (1 site at urban ground level), over 3 sampling days, for 3 site types). Bars represent 95% confidence intervals.

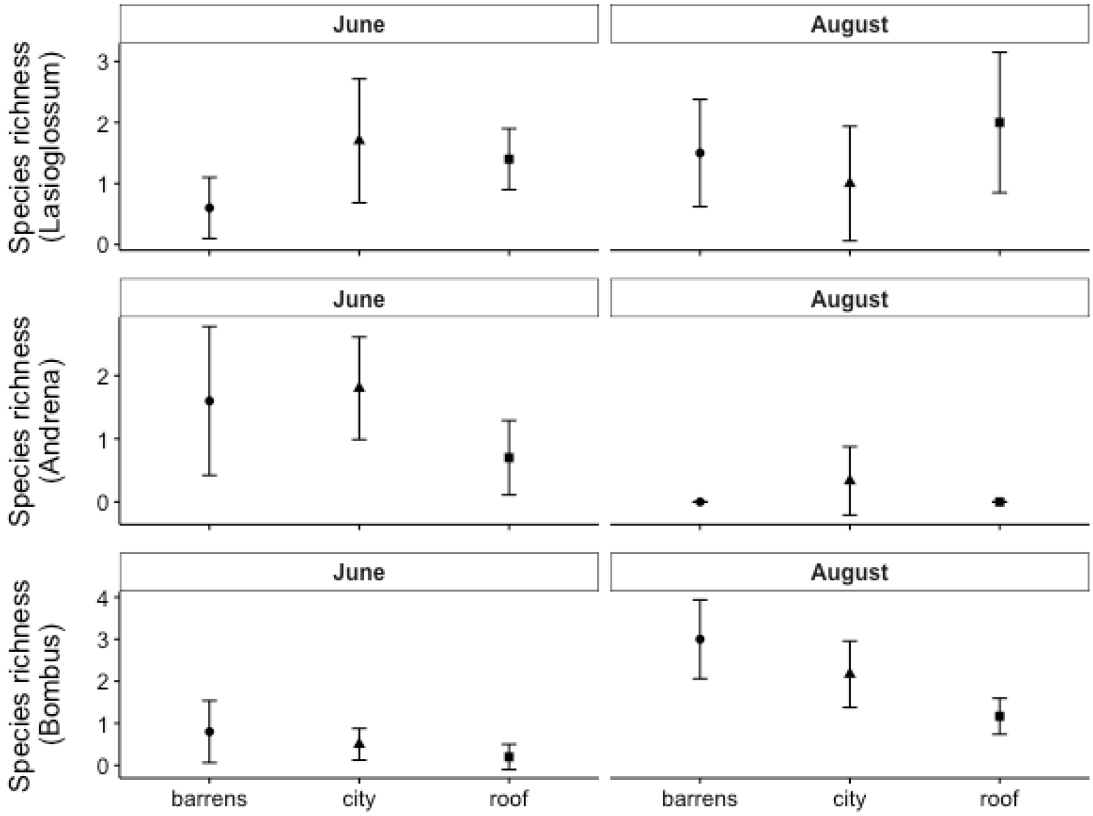

Figure 7. Average daily species richness of the three most common genera (*Lasioglossum*, *Andrena*, and *Bombus*) collected at all sampling locations in June (*n* = 2 sites, over 3 sampling days, for 3 site types) and August (*n* = 2 sites (1 site at urban ground level), over 3 sampling days, for 3 site types). Bars represent 95% confidence intervals.

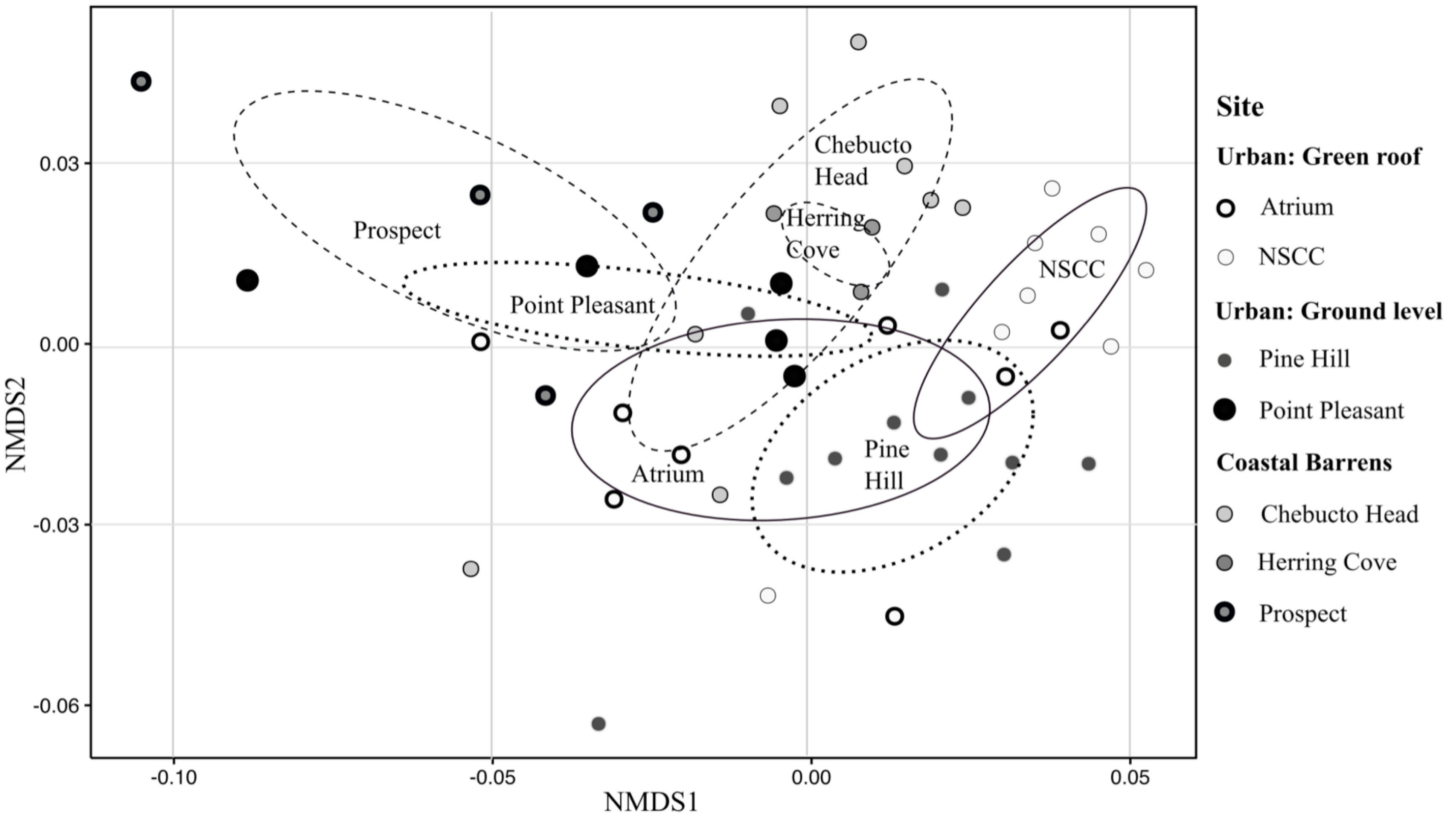

Figure 8 NMDS ordination of bee species abundances across sampling periods by site; June (n = 2 sites, over 3 sampling days, for 3 site types) and August (n = 2 sites (1 site at urban ground level), over 3 sampling days, for 3 site types) data combined. Ellipses represent 95% confidence regions; data centered on axes means, singletons removed**.**

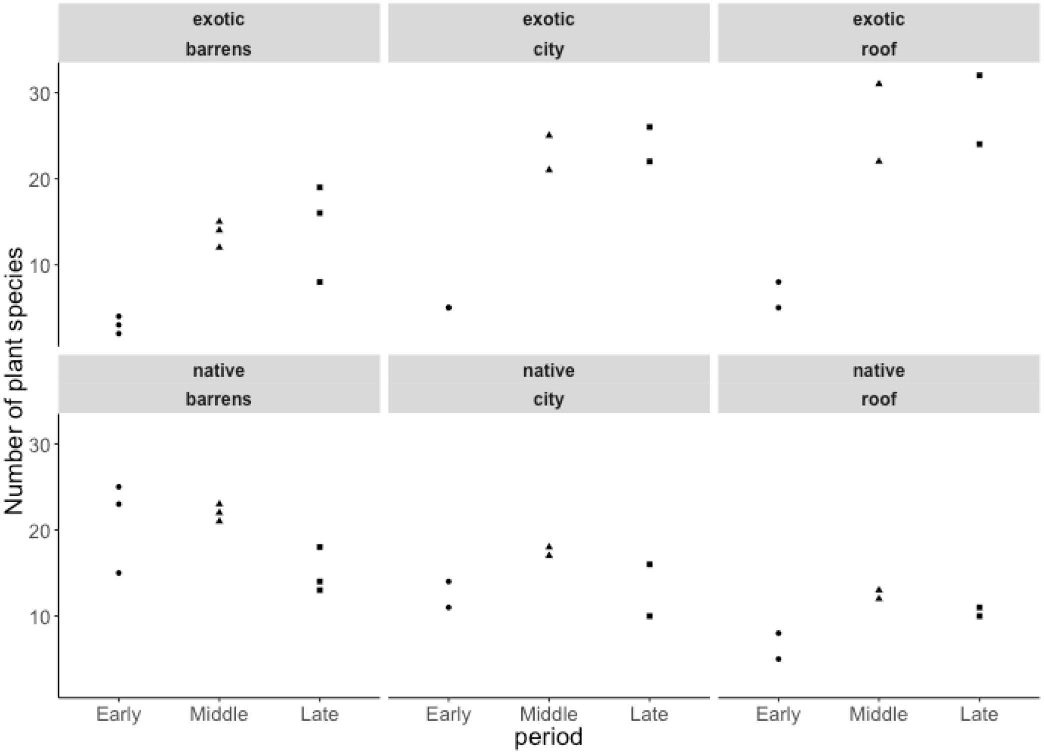

Figure 9. Richness of flowering plant species according to summer period and plant nativity.

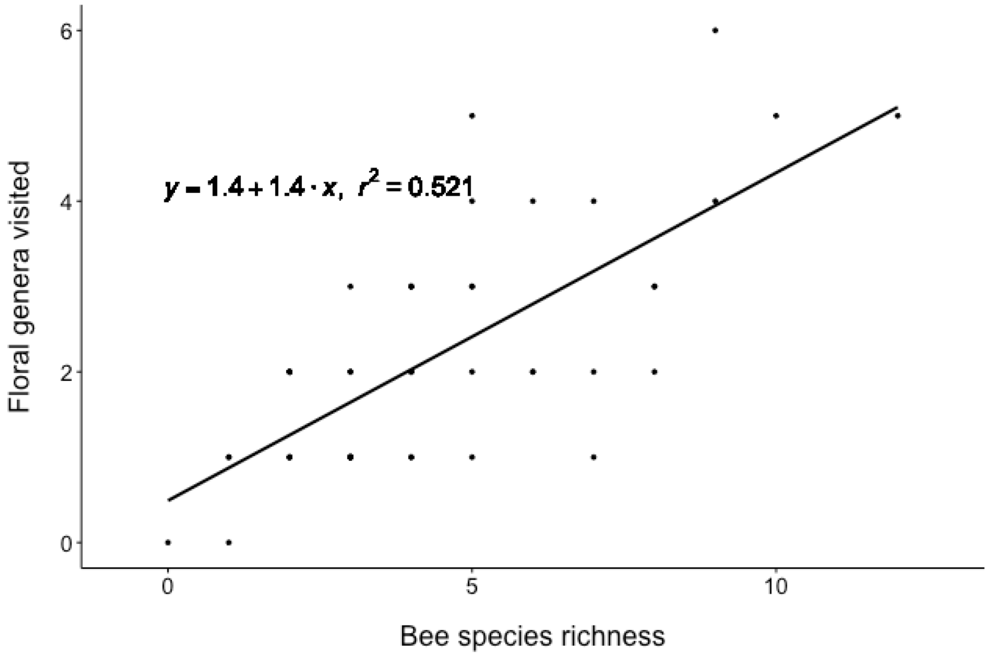

Figure 10. Relationship between bee visitor species richness and generic richness of floral hosts visited, with only those floral hosts on which bee species were captured included (*n* = 48 samples).

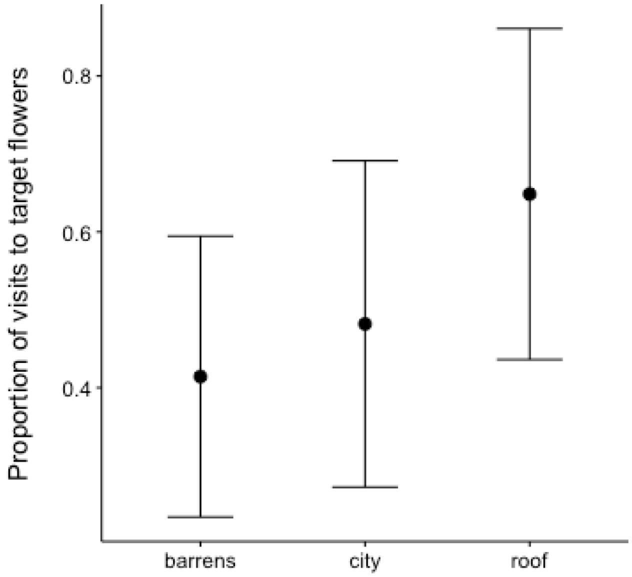

Figure 11. Proportion of bees captured on focal plant species versus all other plant species, by site type (*n* = 16 per site type). Bars represent 95% confidence intervals.

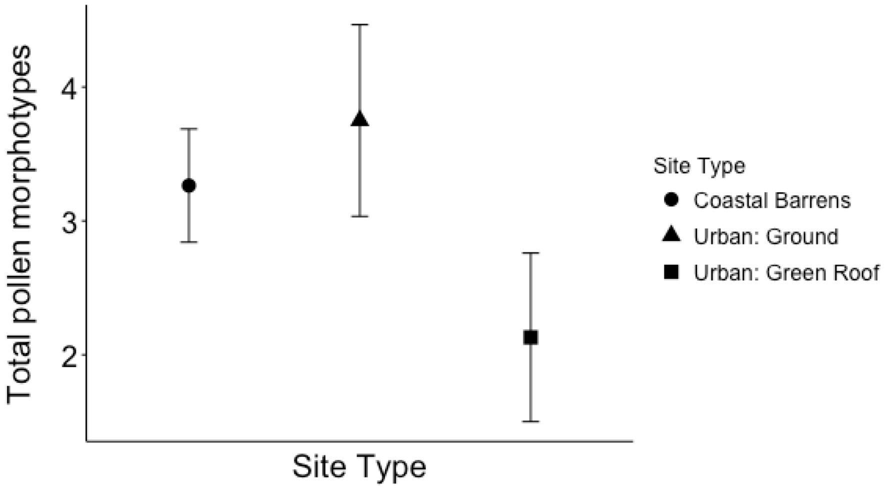

Figure 12. Daily total pollen taxa collected per bumblebee at green roof (*n* = 2 green roofs for 3 days (22 loads)), urban ground level (*n* = 1 urban ground level site for 6 days (43 loads)), and coastal barrens (*n* = 2 coastal barrens for 3 days (67 loads)). Bars represent 95% confidence intervals.

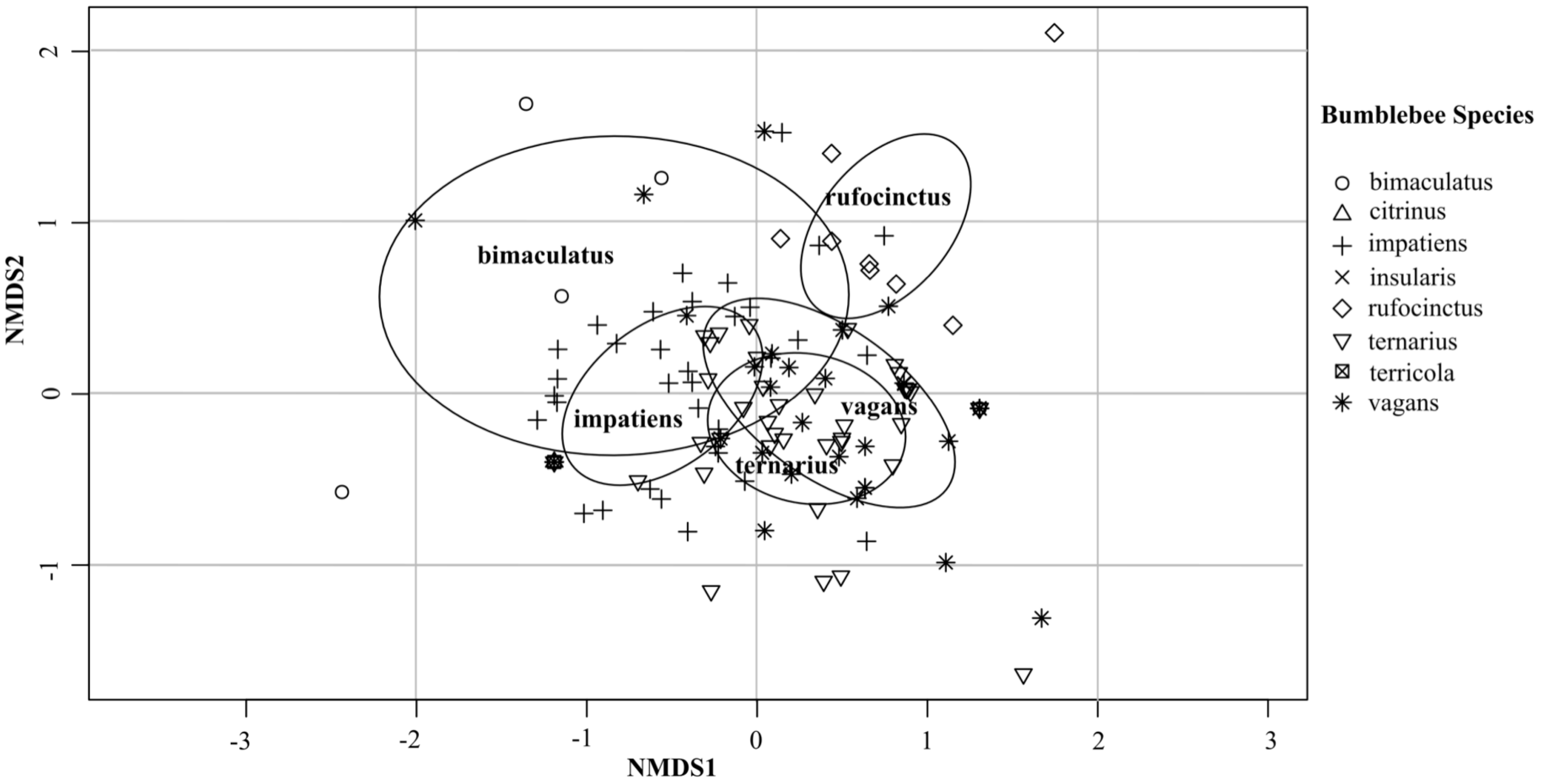

Figure 13. NMDS ordination of pollen taxa contained in bumblebee-collected pollen loads across sampling periods and sites (*n* = 2 green roofs for 3 days, *n* = 1 urban ground level site for 6 days, *n* = 2 coastal barrens for 3 days). Ellipses represent 95% confidence regions for each bumblebee species mean; data centered on axes means, singletons removed.

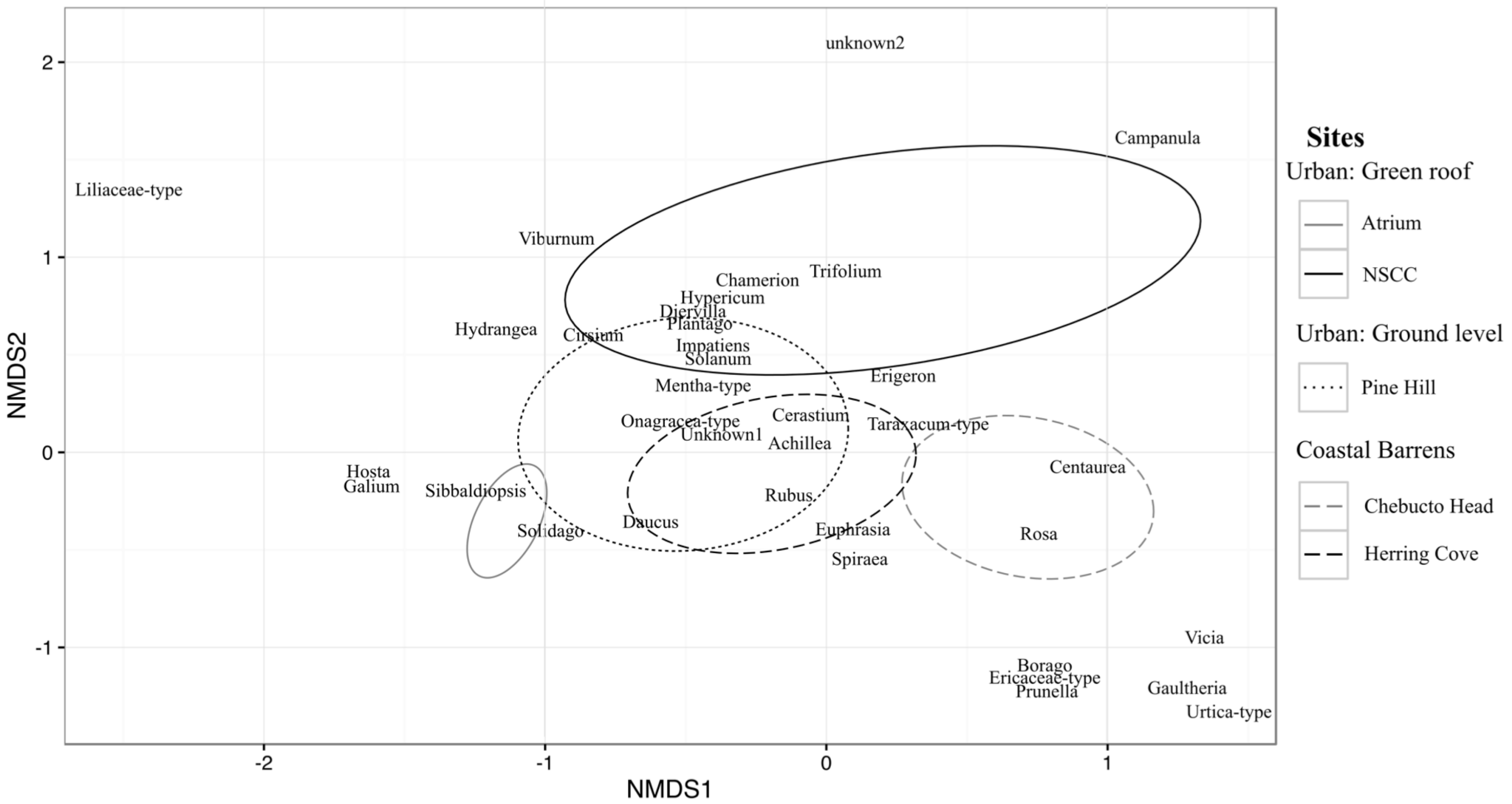

Figure 14. NMDS ordination of pollen taxa contained in bumblebee collected pollen loads across sampling periods and bumblebee species (*n* = 2 green roofs for 3 days, *n* = 1 urban ground level site for 6 days, *n* = 2 coastal barrens for 3 days). Ellipses represent 95% confidence regions for each site mean; data centered on axes means, singletons removed

Chapter 4:

Synthesis: Green roofs as urban habitat for seedlings and wild bees

Thesis synthesis

Development of the modern cityscape has involved the large-scale interruption of ecosystem services provided in pre-disturbance environments. Given the limited allocation of green space in city centres, architects and engineers responded to this loss of urban service provisioning, in part, by designing multifunctional green roofs that could be installed on pre-existing buildings ('retrofitted'). While retrofitting simplifies the green roof construction process, it also constrains the design of extensive green roofs.

Designers planning extensive green roofs suited to retrofitting must add a limited amount of artificial growing medium to the rooftop to abide by loading restrictions (FLL 2008). Accordingly, the plants introduced to this environment experience significant environmental stresses resulting from the shallow substrate depth. In the summer, stress takes the form of water limitation, excessive solar exposure, and/or substrate heating; in the winter, roofs located in northern climates experience subzero temperatures and freeze/thaw cycles (Oberndorfer et al. 2007; Bovin et al. 2001). Due to the simplicity and homogeneity of most extensive green roof designs, this harsh growth environment has placed unsurprising limitations on the suitability of plant species for inclusion in this form of green infrastructure (Dunnett & Kingsbury 2004). However, the emerging role of vegetation richness and specific composition in modifying green roof ecosystem service delivery (Lundholm et al. 2010; Lundholm 2015; Van Mechelen et al. 2015) necessitates the development of extensive green roof designs that facilitate the establishment and maintenance of functionally diverse plant assemblages.

Diversifying the green roof environment

In response to this need for optimized green roof designs compatible with retrofitting, the second chapter (first manuscript) of this thesis detailed a bipartite investigation of the responses of green roof substrate and native seedling communities to several simple design modifications aimed at alleviating some of the environmental stresses associated with the challenging growth environment of green roofs. Substrate temperature and moisture and seedling density, richness, and community composition were quantified at locations associated with specific features (logs, pebble piles, topographic maxima and minima) intended to increase environmental heterogeneity on an extensive green roof at Saint Mary's University. This field investigation was complemented with a greenhouse trial that monitored changes in substrate conditions, seedling density, and species richness during a sustained drought imposed on green roof modules with (or without) surface features shared with the field experiment.

Results presented here indicate that the addition of small amounts of substrate and the presence of easily installed surface features can significantly impact green roof growth conditions by decreasing substrate temperature and slowing moisture loss, creating a more heterogeneous green roof environment. Some of these heterogeneous microsites improved seedling survival and facilitated species persistence relative to the homogeneous green roof microsites that represented conventional green roof conditions. In North America, many native plants fail to persist on conventional extensive green roofs characterized by shallow (<10 cm) substrate and a lack of supplemental irrigation (Dvorak & Volder 2010). However, some species can establish when grown in shaded locations (Dvorak & Volder 2010). Several of our microsites cooled substrate as much as, or more than, the shadiest rooftop areas; this suggests that on roofs not receiving shade from surrounding buildings and upon which large features (e.g. solar panels, see Bousselot et al. 2013) cannot be installed, the inclusion of small, low-maintenance features, such as logs and pebble piles, along with minor increases in substrate depth (total depth of 12 cm) and variation in substrate topography, has the potential to significantly improve seedling survivorship and delay species loss.

These modifications could facilitate the establishment of species rich native plant assemblages, thereby improving the habitat value and functionality of urban green roofs (Cook-Patton & Bauerle 2012; Lundholm 2015). Recent research has highlighted the importance of intra-roof environmental variation (provided by shade gradients) in influencing mature green roof plant dynamics (Buckland-Nicks et al. 2016). To optimize the effects of features tested in this experiment, roof designs must be informed by the idiosyncrasies of the broader roof environment present at each site. Furthermore, our findings hint at the possibility that uncomplicated design modification may alter seedling community composition among the distinct sites created on green roofs; however, more research is needed to confirm this trend as we did not detect a significant difference in total species richness of communities establishing under heterogeneous versus homogeneous green roof conditions. While the short-term studies described here suited the life-stage under investigation (seedling), they did not quantify the long-term effects of these features on green roof plant community development. Research monitoring plant community dynamics through multiple growing seasons would better characterize the seasonality of observed effects and the potential for community diversification associated with the features tested here.

Habitat provisioning for urban bees

Green roofs that support diverse plant communities may optimize ecosystem service provisioning for municipalities and also represent patches of green space in a disturbed and fragmented landscape; as such, they may provide habitat to both green roof plants and urban fauna. However, relationships between rooftop visitors (or colonizers) and green roof resources remain poorly characterized (Ksiazek et al. 2012; MacIvor et al. 2015). Chapter three (second manuscript) of this thesis described replicated field surveys that characterized wild bee communities frequenting green roof, ground level urban, and coastal barrens habitat in Halifax, and directly examined green roof resource use via bumblebee pollen load analysis.

The results indicate that even though the two green roofs sampled in Halifax hosted less abundant and less species rich bee communities relative to local ground level sites, they contained key species present in both natural and urban ground level habitat. Additionally, bumblebees did forage for pollen from green roof flowers, and their pollen preferences appeared to reflect the forage available in the urban matrix and that typically present in natural coastal barrens – including both native and exotic floral hosts. Studies have indicated that bumblebees, which employ a generalized foraging strategy, utilize diverse resources irrespective of plant nativity (Jha et al. 2013; Larson et al. 2014; MacIvor et al. 2015), while others have observed increased attractiveness of native hosts in urban habitat (Fukase & Simons 2016). Thus, bumblebees and other generalist bee taxa common to the urban environment may benefit from diverse and abundant green roof vegetation blooming throughout the summer, especially when mixes include attractive native species. Provision of floral hosts attractive to bee species known to be in decline and observed to forage in urban habitat, such as *Bombus terricola*, may improve the conservation value of green roofs. The effect of attractive exotic floral hosts (e.g. *Centaurea nigra*) on bee pollination services in natural coastal barrens deserves further investigation, given the unique plant communities present and the occurrence of rare plant species in this habitat type (Cameron & Bondrup-Nielsen 2013; Oberndorfer & Lundholm 2009; Porter 2013).

The results of this study reveal the value of pollen analysis in determining wild bee resource use on green roofs, but nectar availability and quality also influence foraging decision-making and patch selection and should be considered in future studies of green roof bee communities. Commonalities in the high abundance (*Lasioglossum*) and near absence (*Ceratina* and *Augochlorella*) of specific bee taxa (Colla et al. 2009; Tonietto et al. 2011) suggest that the value of green roof habitat to urban bees may be linked to forager body size, nest proximity to or installation on green roofs, and ground level floral resource provisioning. Specifically, the results from this study and others (Colla et al. 2009; Tonietto et al. 2011) suggest that some green roofs may only support small-bodied bees that successfully nest directly on the roof; small-bodied bees that must repeatedly fly to the green roof to forage may perceive diminishing returns on their metabolic investment in green roof access. Larger bees, such as bumblebees, may not need to nest on the green roof to benefit from the floral resources present – however, the attractiveness of green roof forage will be assessed relative to the quantity and quality of floral resources available at ground level locations. Thus, these larger bees may repeatedly visit green roofs only when flowers are abundant and provide high quality forage.

Supporting green roof flora and fauna

The features incorporated into the green roofs studied here, which promoted seedling survival and species persistence, have also been recommended for inclusion in biodiverse roofs intended to promote faunal diversity, and at least one study (Brenneisen 2006) indicated that topographic heterogeneity can promote increased invertebrate diversity. It is possible that carefully considered designs that increase environmental heterogeneity may not just improve green roof functionality through plant diversity, but may also provide diverse nesting opportunities and higher quality foraging sites for wild bees and other urban invertebrate taxa. The instability of collembolan populations on green roofs (Rumble & Gange 2013) and the responsiveness of low-mobility arthropod populations to local roof conditions (Braaker et al. 2014) suggest that even small-scale changes, such as those tested here, could have an impact on the value of green roofs to low-mobility taxa.

Mobile organisms may also benefit from local habitat modifications. For example, Cane (2015) found that pebbles similar to those used in this study increased nest presence of ground-nesting halictids at ground level locations. Increased nesting opportunities for small-bodied bees, such as halictids, may facilitate their use of green roof resources by reducing energy expenditure during foraging trips, and selection of plants that provide abundant, high quality pollen and nectar may increase green roof attractiveness to large bodied bees. At least two coastal barrens species that have proliferated on local green roofs tested here, *S. tridentata* and *S. bicolor*, contribute to roof cooling (MacIvor & Lundholm 2011), have demonstrated persistence on rooftops (MacIvor & Lundholm 2011), attracted several bee taxa in this study, and, in the case of *S. bicolor*, have been shown to represent an important source of pollen for urban bumblebees foraging on local green roofs. Results such as these suggest that generating and harmonizing knowledge of microsite preferences of functionally superior green roof plant species and nesting and foraging preferences of important urban taxa, such as pollinators, will yield improved green roof designs that support multi-trophic urban biodiversity and ecosystem service provisioning simultaneously.

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