Evaluating the Habitat-Template Approach Applied to Green Roofs

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Abstract - The habitat-template concept is meant to help select plant species for use in artificial ecosystems by seeking out locally occurring habitats that share environmental conditions with the target artificial ecosystem. For green roofs with shallow growing media, appropriate habitat templates might be found in local exposed, rocky, or otherwise infertile habitats. Many studies report plant selection using this process, but recent research suggests that it may fail for green roofs in extreme climates. In this review, we identify ecological novelty as a potential challenge to the habitat-template approach, and demonstrate that the tendency to focus solely on abiotic conditions may result in species selection biased toward generalists. We propose that trait-based species-selection and attention to the finer details of a given habitat template, including companion species, are worthwhile approaches to successfully diversify plant assemblages on green roofs.

Introduction

Successful rooftop greening must strike a balance between conflicting design constraints because features that create a supportive growth environment for plants may exceed the structural capacity of a building. The placement of soil and vegetation on top of a building adds to the weight loading of the roof. As a consequence, many green roofs incorporate artificial substrates that are shallower than the soils occupied by most native vegetation communities in the region. These "extensive" green roofs thereby present challenges to plant survival due to the relatively harsh abiotic conditions associated with shallow soil depths and rooftop exposure. For over a century, designers of temperate-zone green roofs have focused on drought-tolerant species, especially succulents, to maximize plant survival, coverage, and ecosystem services in challenging rooftop environments (Köhler 2006, Köhler and Poll 2010). The original habitats of many of the species (e.g., *Sedum* spp. [stonecrops]) used successfully on extensive green roofs are rocky environments with shallow soil (Lundholm 2006).

Originating in Germany, a green roof industry catering to the needs associated with rooftop plant establishment has developed in the last 40 years, formed of companies that supply specialized growing media, engineered components, and plants for green roofs. Over the last 2 decades, green roofs have gained popularity in North America, and several major European companies have set up North American branches to take advantage of these new markets. The established firms and start-ups primarily relied on a palette of plant species tested in Europe, dominated by

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succulent species native to Europe and Asia (Dvorak and Volder 2010). The industry relies on succulents because these species survive better than other life forms under the hot and dry conditions typically found on green roofs (Monterusso et al. 2005, Rayner et al. 2016, Rowe 2015) and also recover better from severe drought (Bousselot et al. 2011). Many of the green roof companies operating in North America have developed regionally specific plant mixes to satisfy the demand for native species of a variety of life forms (Butler et al. 2012).

While the increasing popularity of native plant species in ground-level landscaping motivated the development of these green-roof native-plant mixes, plant diversity also influences ecosystem service provisioning by green roofs. Green roofs are multifunctional ecosystems, and, although succulents perform some functions well, a greater diversity of plant life-forms may be important to provide a full range of services. For example, grasses may perform stormwater-retention functions better than succulents because they have high water-demand and their taller canopies may intercept more rainfall (Dunnett et al. 2008, Nagase and Dunnett 2012). Consequently, plantings that combine life forms with different resource-use strategies can promote improved provision of multiple ecosystem-services by green roofs (Lundholm 2015a).

Choosing plant species that will survive on green roofs is essential to maintaining aesthetics and performance because vegetation dieback leads to functional impairment (Speak et al. 2013) and may result in additional economic costs for installers or owners. Beyond their thermal and hydrological services, green roofs provide habitat for many spontaneously colonizing organisms, including insects that are rare or otherwise important for conservation (Jones 2002, Kadas 2006). Green roofs that contain a greater variety of floral resources are expected to provide habitat of greater value for pollinators and other invertebrates (Williams et al. 2014) than roofs with lower species or life-form diversity. These functional considerations provide further motivation for selecting plants in addition to succulents for use on green roofs.

Given that North America has a diversity of habitats that feature shallow soils and high plant-biodiversity, Lundholm (2006) recommended the habitat-template model as an ecological approach to selecting a variety of plant species for use on extensive green roofs. The habitat-template, or habitat-analog approach exploits what urban ecologists have known for decades: that some species are preadapted to urban or other artificial environments because they evolved in natural habitats with similar characteristics (e.g., Gilbert 1989, Wittig 2004, Woodell 1979). Thus, searching for local habitats that share similar abiotic conditions with green roofs provides a potential method for finding suitable species for green roofs, representing biomimicry at the ecosystem level (Pederson Zari 2016). Many researchers and designers of constructed ecosystems have incorporated these ideas into green-roof plant selection on several continents (Fig. 1; MacDonagh and Shanstrom 2015, Van Mechelen et al. 2014a, Williams et al. 2010), and the concept applies to a range of other urban and industrial ecosystems (Lundholm and Richardson 2010). The goal of this paper is to evaluate this concept as it applies to green roofs 10 years after the publication of the original "habitat template" paper in *Urban Habitats* (Lundholm 2006). We also delve further into the concept of ecological novelty and outline how this approach may inform the ecological engineering of green roofs and other constructed ecosystems.

Empirical Tests of the Habitat-Template Approach

There is little doubt that the broad concept of a habitat template for green roofs has validity: the succulents typically used on extensive green roofs have their origins in relatively extreme habitats such as rock barrens, cliffs, or deserts. However, the general applicability of the habitat-template approach in sourcing non-succulent species suited to green roofs from local habitats is unclear. Many recent studies encompassing different climate zones report the use of habitat-template or analog concepts to identify suites of plant species suitable for inclusion in extensive green-

Figure 1. Examples of natural habitat templates and corresponding green roofs. (a) coastal rock barrens, Izu Peninsula, Japan, with (b) corresponding green roof; (c) dry grassland, Victoria State, Australia, with(d) corresponding green roof; (e) Mediterranean scrub, Athens, Greece, with (f) corresponding green roof; (g) coastal heathland, Nova Scotia, Canada, with (h) corresponding green roof. Photographs © J. Lundholm.

roof designs (e.g., Caneva et al. 2015, Kinder 2009, Myers 2012, Van Mechelen et al. 2014a) and emphasize regionally specific vegetation types as sources of plants (e.g., Natvik 2012, Williams et al. 2010). This approach has generated several regional lists of candidate green-roof species, but not all taxa have been experimentally validated (Caneva et al. 2015, Myers 2012, Van Mechelen et al. 2014a).

Overall, the concept fits with the idea that shallow substrates place key abiotic limits on the survival of plant populations in extensive green-roof systems. One of the most detailed evaluations of the habitat-template concept for green roofs (MacDonagh and Shanstrom 2015) indicates that careful attention to the details of species requirements, with empirical testing on multiple roofs, results in a selection of native species that survive on roofs for at least a decade and likely much longer. Van Mechelen et al. (2014a, b) describe how the habitat template approach can be combined with a functional-trait approach to derive useful plant lists for a given region. However, recent work also indicates that sourcing plants from a local habitat characterized by severe drought and shallow substrates may not be sufficient to ensure survival of non-succulent taxa on green roofs. Rayner et al. (2016) evaluated a range of plant species representing several life forms, all native to drought-prone habitats from several regions and found that leaf succulence was the best predictor of survival regardless of the source region or habitat of the species. The habitat-template approach may work best as a coarse filter for selecting species, but it can be refined through the use of complementary techniques like functional-trait analysis.

Ecological Novelty

Many drought-prone environments host a variety of plant life-forms, including forbs, graminoids, leaf succulents, shrubs, bryophytes, and lichens. Among vascular plants, succulents are the most drought-tolerant and show superior survival and recovery from drought in many green-roof contexts, outperforming the other life forms (Bousselot et al. 2011, Durhman et al. 2006, Getter et al. 2009, MacIvor et al. 2013, Monterusso et al. 2005, Rayner et al. 2016, Thuring et al. 2010). This finding suggests that the green-roof conditions are harsher than those experienced by many species at ground level in natural habitats within a region. A particular ground-level analog habitat may already represent the most extreme edaphic conditions in which a species can survive; such a species might already be living at its niche margins and may be unable to accommodate additional stress. Green roofs impose stresses similar to those present in natural analog habitats, such as drought and high maximum temperatures, but the magnitude of these stresses may be amplified or reduced on the roof relative to the habitat analog; the character of both the "biophysical envelope" and the "abiotic infrastructure" (Hobbs et al. 2009) of a given green roof may be perceived as distinct from the conditions circumscribed by its local analog. There also may be novel sources of stress in rooftop environments introduced by artificial soil components, urban pests, pollution, or lack of symbionts (e.g., John et al. 2014).

An ecosystem may be designated as novel if it features abiotic or biotic conditions without natural historical precedents; this novelty is maximized following simultaneous and pronounced alteration of both living and non-living components of a system (Hobbs et al. 2009). Recent articulations of the "novel ecosystem" concept suggest that we should use the term "hybrid" for artificial or constructed ecosystems such as green roofs (Hobbs et al. 2013). In that view, the term "novel ecosystem" is reserved for ecosystems that have some historical continuity with a natural or semi-natural habitat, such as those that have been heavily influenced by disturbance by humans or invasive species but are still remnants of some "natural" habitat like a forest or grassland. However, a focus on one level of ecological organization (ecosystem) may obscure key ecological processes occurring at other levels. The habitat-template concept implies a gradient of novelty (Lundholm and Richardson 2010) such that an artificial ecosystem can present conditions similar to those experienced by a plant population in its natural habitat. Although the whole ecosystem may be considered "novel" or "hybrid" because it was created by humans and lacks historical continuity with a natural habitat, the goal of the habitat-template approach is to seek plant species that are suited to the conditions on a green roof, thus reducing the novelty encountered by individuals of a given species that we plant on a roof. This gradient of ecological novelty (Lundholm and Richardson 2010) represents a way of conceptualizing differences between the ecological context in which a plant population evolved and the current setting in which it grows. The habitat-analog idea is intended to inform plant selection by reducing the potential for plants to encounter a novel environment on a green roof in which they are unable to survive. We re-examined the various studies reporting the superiority of succulents over other life forms on shallow-substrate green roofs using an "ecological novelty" lens and found that leaf succulents may show some level of pre-adaptation to the extremes of temperature and soil moisture on green roofs. In contrast, conditions may be too different from those typically experienced in natural areas by plants with other life forms for them to survive on green roofs. Thus, ecologically novel aspects of the green roof act as a strong filter to constrain the plant species that can be grown in these created landscapes.

Despite broad similarities between natural templates and green roofs, the devil may lie in the details, such as soil temperatures on roofs that are more extreme than in natural environments (Rayner et al. 2016). Detailed consideration of the abiotic differences between green roofs and natural habitats may reveal important elements of novelty built in to green-roof habitats. For example, there is a common assumption that rocky habitats are dominated by shallow-rooted species, but recent work shows that a key strategy of some species is to grow long roots that can penetrate cracks in rocks and find water much deeper than suspected when researchers considered average soil depths alone (Poot and Lambers 2008, Schenk 2008). Such species would find green roofs inhospitable because the physical space provided on a green roof does not include narrow cracks that can act as refugia for long roots, and plants with long roots might exploit structural weaknesses that could compromise roof integrity (Archibold and Wagner 2007). Likewise, persistence of plant populations in a particular natural habitat may reflect very different adaptations by different species. Monterusso et al. (2005) compared drought-tolerant succulents with tall-grass prairie forbs and grasses and found that the succulents were generally superior in survival and growth in the green-roof environment. Although both groups of species can be considered drought-tolerant, tall-grass prairie forbs and grasses generally have deep roots, whereas succulents are shallow-rooted. Thus, establishment and survival on a shallow-soil green roof favors a specific kind of drought-tolerant species. The results of Rayner et al. (2016) may also reflect different plant strategies: grasses and forbs from harsh rock-outcrop habitats may require thin cracks in bedrock to survive drought, whereas succulents living in the same habitat likely use stem and leaf morphological adaptations or distinct physiology (e.g., CAM photosynthesis) to survive. Altering the design of artificial ecosystems to render specific abiotic conditions more suitable for constituent species may reduce the novelty experienced by plants and any associated fauna, giving them a better chance of survival (Lundholm and Richardson 2010). Simple habitat modifications, such as the addition of coarse woody debris, gravel piles, or soil mounds, can greatly reduce maximum summer temperatures on a green roof and slow water-loss rates (Walker and Lundholm, In press), possibly allowing species with a greater range of traits related to drought or high-temperature tolerance to persist on a given roof. However, for green roofs in hot, dry regions, some climatic features, such as high substrate temperatures (Simmons 2015), may be difficult to mitigate without irrigation or other measures that are economically or environmentally costly.

Generalist species are likely to tolerate a broader range of abiotic conditions (Simmons 2015) than specialists, and thus, might be expected to have a better ability to tolerate novelty, so the coarse habitat-template approach may be more likely to select appropriate generalist species. We should also acknowledge that some specialist invertebrates can spontaneously colonize green roofs (Jones 2002, Kadas 2006), but planning green roofs for a greater diversity of habitat specialists will likely require much greater attention to the details of the particular resource and nesting requirements of these species. Attempts to build habitat heterogeneity into green roofs (Brenneisen 2006, Molineux et al. 2015, Olly et al. 2011) can be viewed as attempts to increase the ecological similarity between natural habitats and green roofs, such that a greater range of more specialized species can find appropriate habitat on green roofs (Best et al. 2015, Dunnett 2015). Similarly, habitat features, such as human-made "bee hotels", may be designed to resemble natural nesting substrates for a variety of solitary cavity-nesting bees (MacIvor and Packer 2015). At a coarse level, bee hotels are engineered to imitate the physical dimensions of natural cavities used by various bee species, but if the materials used for their construction do not functionally approximate the thermal or hydrological performance of natural cavities, they may only support common urban generalists or adaptable introduced species (MacIvor and Packer 2015). Just as bee hotels may fail to adequately mimic natural nesting conditions for native bees, green roofs may represent abiotic conditions that are too extreme, relative to their associated habitat analogs, to support the same range of plant life -forms or diversity of invertebrates and instead may favor weedy, common, or generalist taxa.

Biotic Interactions

The habitat-template concept assumes that abiotic factors are the most important in limiting the kinds of plants that will survive on extensive green roofs. This assumption is generally consistent with broad ecological theory (e.g., Grime 1973), which links low-productivity habitats with stress-tolerant plant species as a result of strong selection pressures related to low resource availability and harsh conditions. However, competition or facilitation between plants, as well as herbivory, can also be important even in infertile environments (McGraw and Chapin 1989, Reader 1998); hence, the habitat-template model may also ignore key features of the biotic environment that place limits on plant success. Biotic interactions may also be novel relative to what plants experience in their "home" environment, such as when herbivores that normally consume substantial amounts of biomass are absent from the system (Keane and Crawley 2002), or when pollinators or other species that facilitate the success of plants are missing (Parker 1997), resulting in positive or negative effects on plant growth and survival.

Differential presence of plant enemies may be a common form of ecological novelty experienced by green-roof plants. Pests such as herbivorous insects and fungal pathogens are likely affected by many aspects of the green-roof environment including availability of alternate habitats at ground level, overall abundance of hosts in the neighborhood, dispersal limitations, and availability of organisms at other trophic levels that might control pest populations. It is easy to imagine scenarios where certain pests are more abundant on rooftops than in natural environments. On green roofs in Halifax, NS, Canada, aphid pests were more abundant on native plants on the roof compared to their natural habitats, possibly due to lack of salt spray usually present in coastal environments or absence of predators that reduce aphid populations in natural areas (Grimshaw-Surette 2016). However, body size and roof height may limit the dispersal of some insects to green roofs (MacIvor 2016) thus, reducing colonization rates of both pests and their parasites (or predators) relative to ground level, as has been observed in a forb–leaf-miner parasitoid complex (Quispe and Fenoglio 2015). Additionally, there is much evidence to suggest that many invasive species benefit from enemy release. In their invasive range, these species have escaped predators that would have controlled their population growth in their native range (Keane and Crawley 2002). Given the possibility that green roofs are relatively isolated from their analog habitats and may have other novel features, both native and non-native plants might experience enemy release on rooftops, possibly leading to greater productivity and performance of ecosystem functions. This possibility highlights the potential of novelty in the biotic conditions, but also abiotic conditions, to result in positive effects on plants. For example, plants may perform better in the roof environment than in their typical natural habitat due to enhanced resource availability or other differences (Lundholm et al. 2015). Both negative and positive consequences of novelty should be considered in attempting to understand plant performance on green roofs.

Vascular plants living in dry, low-nutrient habitats often coexist with other autotrophs such as bryophytes and lichens, and these associated species might play a role in facilitation of vascular plants (Heim et al. 2014) by, e.g., reducing the physical stress caused by harsh conditions (Bertness and Callaway 1994, Butler et al. 2011), but other, more intimate interactions, such as root-microbe associations, may be essential for the survival of some plant species. Commercial green-roof substrates may initially be devoid of mycorrhizal fungi (John et al. 2014), which is a condition that may represent another novel feature of green roofs based on artificial substrates (Best et al. 2015). This absence may limit the success of some native species (Schroll et al. 2011). DNA sequencing of samples from green-roof substrates has revealed the presence of diverse fungal communities (McGuire et al. 2013), but without further characterization of the ecological roles of constituent species or the relative abundance of key functional groups (e.g., root mutualists, litter decomposers, pathogens), the contribution of spontaneously colonizing soil microbiota to green-roof ecology and performance remains uncertain. Soil microbes play key roles in ecosystem functions, such as soil stabilization (McGuire et al. 2015), that also indirectly influence plant survival. Thus, both abiotic and biotic substrate characteristics are important in determining whether a particular plant species can survive on a roof. Use of natural soils and plants from the same site may promote better plant performance through provisioning of local soil symbionts, pre-established seed banks, or favorable mineral compositions (Best et al. 2015, McGuire et al. 2015). Use of native soils may be one explanatory factor in the long-term success of the sod roofs of northern Europe, which are created by moving entire sods, including soil, soil organisms, and plants to roofs (Best et al. 2015, Natvik 2012). For roof designs that cannot accommodate natural soils, substrate inoculation with bacteria or fungi appears to be a promising option for promoting soil symbionts (Molineux et al. 2014, Young et al. 2015). The increasing awareness of the importance of plant–microbe interactions and their specificity suggests that the habitat-template model is incomplete without consideration of the entire biological community interacting with plants in a given habitat. Adding plants to a green roof without companion species will lead to a biased selection of species that do not require mycorrhizae, facilitation, or other positive interactions with other species. *Sedum* spp. are usually non-mycorrhizal, which may help to explain why these plants are often successful in typical temperate-zone extensive green roofs with artificial substrates (John et al. 2014).

Although these ecological interactions are important, interacting populations also impose evolutionary selection pressures on one another. Many studies have revealed that coevolution among competing plant species and between plants and other organisms is extremely local and may lead to genotypic variation caused by competition among different plant species within a single pasture (Turkington 1979, 1989). Plants are adapted to microhabitat conditions, including their biotic neighborhood; thus, maximizing plant success on green roofs might best be done at a community level, as opposed to the selection of species that might not usually grow together. This trend toward marked local adaptation further suggests that plants from specific populations are adapted to each other; selection of the same plant species within a region may yield different results when 2 species are grown together on a green roof, depending on whether their source populations interacted in their evolutionary history. Recent work on species introductions shows that local adaptations can evolve very rapidly (Oduor et al. 2016), and effects of coevolution on resource use and ecosystem functions, such as biomass production, can also develop quickly (Martin and Harding 1981). There is much recent interest in designing biodiverse roofs to improve certain functions related to resource use such as stormwater and nutrient retention (e.g., Johnson et al. 2016, Lundholm 2015a, Nagase and Dunnett 2012); plant population origin may represent a neglected component of such studies. Given the potential for rapid evolution in novel environments, the habitat-template approach need not rely on purely "natural templates", but can include completely artificial habitats. Some biodiverse roofs in the UK adopted rubble fields ("brownfields") as a template (Baumann and Kasten 2010, Dunnett 2015, Kadas 2006) due to their ability to support urban biodiversity (Gibson 1998, Lorimer 2008), while others have mixed natives and introduced species or contain only introduced species. Finally, with the growing recognition that interspecific coevolutionary processes are important to individuals, populations, communities, and ecosystems, and given the rapidity at which evolutionary change can occur, it could be argued that old green roofs (e.g., Köhler 2006, Köhler and Poll 2010, Lundholm 2015b, Rowe 2015, Thuring and Dunnett 2014) themselves may be the ultimate habitat template for new green roofs in a particular region because they might now contain assemblages of plants, microbes, and other interacting species that have coevolved to survive and prosper on green roofs.

Conclusions

The goal of this paper was to evaluate the habitat-template concept for green roofs from the perspective of modern ecology. Plant selection is relevant to many aspects of green-roof ecology. There are numerous cases where the habitat-template approach has been used to successfully select plants for extensive green roofs in different environments; there are also cases where it has proved inadequate. Within a framework of ecological novelty, the habitat template approach seeks to minimize the novelty of the abiotic infrastructure to promote long-term vegetation persistence. The habitat-template approach is probably best used as a coarse filter for plant selection on green roofs; several factors imply that a more nuanced approach is required in some settings. The abiotic and biotic environments on a green roof may be too novel for a given plant population to succeed. Trait-based protocols have been productively used to give a finer resolution for selection of plant species, and it makes sense to combine both approaches. Another method is to extend the habitat-template approach even further, by not only identifying appropriate plant species based on local habitats, but by including entire communities and providing replication of the abiotic components of these habitats. While this protocol may not be feasible for green-roof designers due to logistic constraints, it may be important to employ it if habitat creation for specialist taxa is a priority for a particular roof project. The ecological novelty associated with green-roof systems may also lead to positive effects on ecosystem functioning. Considering these features may lead to ecological insights and could help engineer better-performing green roofs.

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