Green Roofs and Facades: A Habitat Template Approach

by Jeremy T. Lundholm

Saint Mary's University, Department of Biology/Environmental Studies Program,
Halifax, Nova Scotia, B3H 3C3 Canada

Abstract

Extensive green roof habitats are characterized by shallow substrates and extreme soil-moisture conditions. This set of characteristics, or "habitat template," has natural analogs in rock barren ecosystems such as cliffs, scree slopes, and limestone pavements. Typical plants used in green roof initiatives often have their origins in rocky habitats, as do a host of other common urban species. This paper examines the implications of using natural ecosystems as templates for green roof design. While green roof plant selection has targeted drought-tolerant species, the incorporation of other features of rocky habitats may improve green roof functions.

Key words: biodiversity; biomimicry; community ecology; drought tolerance; ecosystem functions; green buildings; rock outcrops; stormwater; urban ecology

Green Roofs and Facades as Habitats

The use of plants on building surfaces has a long history, stretching back at least to the legendary Hanging Gardens of Babylon (Larson, Matthes, Kelly, Lundholm & Gerrath, 2004). Incorporation of vegetation on the surfaces of "green buildings" has a more recent pedigree, revolving around the functional benefits of plants to building performance. The impact of urban development on natural ecosystems is severe due to habitat replacement and the amount of energy and materials required to sustain the built environment. Recent approaches to mitigating this damage include the development of technologies to increase the efficiency of building energy use and decrease the export of waste products out of the built environment. Green roofs provide a variety of services to the urban environment, including visual relief, accessible green space, stormwater retention, reduced building energy consumption, and habitat provision for other organisms (Dunnett & Kingsbury, 2004). The vegetation of typical modern cities tends to be composed of remnant patches of pre-urban habitats and spontaneously colonized sections such as vacant lots and pavement cracks.

Modern cities are dominated by the built environment, which contrasts with the original habitats it replaced through its high density of hard surfaces. This salient feature of the built environment can have a number of ecological impacts. Urban habitats are often too dry for substantial vegetation because of shallow or nonexistent soil; or they may be too wet as a result of inadequate drainage caused by the impermeability of hard surfaces (Aey, 1990; Spirn, 1984). The downstream effects of hard surfaces are evident after rainfalls: Most of the water runs off the built environment, and this leads to rates and volumes of water flow that are much greater than in most other ecosystems, where soil intercepts and retains much of the precipitation (Jennings & Jarnagin, 2002). Dark hard surfaces have lower albedo (reflectivity) than vegetated surfaces; buildings with these hard surfaces have high rates of heat absorption and require a high expenditure of energy for summer cooling in temperate regions. The addition of vegetation and soil to hard surfaces mitigates many of these effects.

Plants used to provide ecological functions—such as temperature modification and precipitation interception—on flat building surfaces or walls are typically those adapted to drought-susceptible, shallow-soil environments (Dunnett & Kingsbury, 2004). This is a function of the practical limits of increasing the load on rooftops. While intensive green roofs or "roof gardens" are built to contain small areas with up to a meter of growing medium and luxuriant vegetation, the more economic and widely applied extensive green roofs minimize substrate depth. This latter approach places strong constraints on the vegetation of living roofs (shallow substrates over hard surfaces can mean both drought and flooding during the growing season). To design for the complexities of functioning plant communities in relatively harsh environments on buildings, we need to deal explicitly with the habitats where green-building species originated. We need to match plant communities with environmental conditions in the built environment that mimic conditions in their original habitats. Which habitats are these? What are the ecological characteristics of these areas, and how can knowledge of these characteristics help us improve the performance of green roofs? Viewing building surfaces as potential habitats provides a guiding concept for understanding urban environments. In this paper, I outline the habitat template concept as it is understood by community ecologists. I then show how the concept can be applied to urban environments, with specific reference to green roof habitats, in particular the potential benefits of mimicking habitat and vegetation features of natural habitats in green roof design.

Habitat Templates

Most species have existed for hundreds if not thousands of times longer than the first human-built structures at the edges of caves. Species also display associations with particular habitats that contain their optimal conditions for growth, survival, and reproduction. Ecologists classify these habitats by dominant vegetation, the presence of water, or other factors. For instance, marshes, grasslands, alpine meadows, coniferous forest, and dunes represent distinct "habitat types." Some species are highly plastic and tolerant of a range of conditions; however, the fact that no single species occurs everywhere demonstrates the fit between species and their preferred habitats. The term "habitat template" refers to a quantitative description of the physical and chemical parameters that define a particular habitat and separate it from other habitats (Southwood, 1977; Suren & Ormerod, 1998). These conditions shape the evolution of organisms and act as a filter that screens out many potential colonizing species not suited to particular habitats.

Conventional buildings function as habitats for many species that spontaneously colonize their surfaces. From the perspective of green building design, we need to ask what kind of habitat templates we have created with conventional building design and how we can alter these templates to suit the species we want as part of green buildings. What do we already have and how can we improve it? With reference to urban ecosystems and green roofs in particular, the question then becomes: What kinds of habitat templates were exploited by current-day urban species before we constructed buildings?

Urban Habitat Template

Ecologists have been slow to acknowledge urban environments as worthwhile subjects. Urban habitats are often perceived as being too disturbed to generate knowledge about nature (McDonnell et al., 1997), and cities have consequently not been incorporated into mainstream ecological theory (Collins et al., 2000). Studies of urban biodiversity have emphasized the differences between city habitats and surrounding areas (Kunick, 1982), with a particular focus on classifying plant species by their relative ability to colonize human-altered habitats (Hill, 2002; Kowarik, 1990). The dominance of urban areas by nonnative species (Kowarik, 1990) has also fueled the denial of ecological value to these areas. Species diversity typically decreases toward the city center (Alberti et al., 2003), where hard surfaces dominate. Urban-ecology literature also emphasizes the creation of novel environments, especially closer to urban centers, where the built environment dominates the landscape (Aey, 1990; Collins et al., 2000). Most of this work emphasizes disturbance intensity as the primary environmental factor that differentiates biotic communities in natural versus anthropogenic urban habitats (Kowarik, 1990): Areas dominated by the built environment inflict novel selection pressures and harsh conditions on any species that attempts to colonize.

This work tends to ignore the possibility that many urban habitats, while lacking historical continuity with the habitats they replaced, may be (as far as some species are concerned) functionally equivalent to other kinds of natural habitats. Botanists working in urban areas have long recognized that a peculiar set of species tends to colonize hard-surfaced environments in cities (Rishbeth, 1948; Woodell, 1979). These species have varied origins but are often found naturally in rocky habitats, dunes, or other open areas where harsh conditions prevent the formation of forest cover. The habitats offered by buildings and other parts of the built environment tend to lack soil, and thus tree cover seldom develops spontaneously in them. Rooting space available to plants is restricted or compacted, and moisture regimes range from extremely dry to waterlogged due to the poor drainage associated with hard surfaces. These physical factors constrain the pool of available colonists to those that already possess adaptations to similar conditions in nature. Plant species from rocky habitats and other urban-analog environments have adaptations such as drought avoidance (dormancy) and drought tolerance (e.g., succulent leaves) that allow them to survive in such harsh conditions. There is also the case of plants like *Cymbalaria muralis* (note the overt reference to a built-environment template in the species epithet), a cliff-dweller whose flowers orient themselves away from the cliff face—presumably to attract pollinators—but whose fruit pedicels exhibit negative phototropism and promote growth toward cracks in the rock surface, and thus toward suitable microsites for germination. This species actually plants its own seeds!

The first more comprehensive attempts to find natural analogs for urban habitats were led by anthropologists and environmental psychologists who examined the typical suburban landscapes of North America and Europe. They concluded that the suburban landscape copied features of ancestral human habitats on the African savannas—relatively open grassy areas with sparse trees, providing both prospect (the ability to scan the surroundings for food sources or enemies) and refuge (sparse trees) from predators (Orians, 1986; Orians & Heerwagen, 1992) (Figure 1). Such research invokes human evolutionary history in savanna habitats and suggests that our preference for similar landscapes, when we are able to consciously design them for ourselves, is genetically "hard-wired." As the thinking goes, proto-human populations who sought out areas that afforded prospect views and protection would have had better probabilities of survival, and their behavior would have been subject to natural selection. This research articulates the linkages between designed and natural habitats, and argues, in part, for a biological basis to our preference for broad classes of landscapes. While this hypothesis is impossible to test, there is a surprising amount of empirical data suggesting that many modern humans do show innate preferences even for mere pictures of landscapes that contain key features of savanna habitats (Orians, 1986).

This "suburban savanna" hypothesis, however, omits salient features of both current urban habitats and ancestral human landscapes: the built structures themselves. Urban settlements are characterized by hard surfaces of stone, brick, and wood, with little substrate for plant growth (at least on the outside of the structure). Additionally, there is considerable evidence that East African savanna environments would have been inhospitable to early hominids without the scattered presence of rock outcrops to provide shelter (Larson et al., 2004). Thus the suburban savanna hypothesis omits the actual hard-surfaced buildings or shelters from the habitat template.

The Urban Cliff Hypothesis

The widespread creation of hard-surfaced environments and their colonization by species adapted to rocky habitats suggests that urban development is not simply a process of habitat destruction but one of replacement of original habitats by ones that may be functionally and structurally analogous to rock outcrop habitats (Larson et al., 2004). This idea is supported by recent work showing how plant species that have spontaneously colonized urban habitats—including pavements, walls, roofs, and lawns—are disproportionately drawn from rocky habitats (Lundholm & Marlin, 2006). Other original habitats that contribute urban species include riparian zones and lakeshores (Wittig, 2004), as well as dunes, rocky beaches, and grasslands (Rodwell, 1992, 2000). In a recent study in Atlantic Canada (Lundholm and Marlin, 2006), many of the grasslands that contributed urban species were found to be anthropogenic in nature and composed of European species that originally came from permanently open habitats such as cliffs, dunes, and shorelines (Grubb, 1976).

The urban cliff hypothesis predicts that a large proportion of spontaneously colonizing organisms in cities originate in rare and geographically marginal rock outcrop habitats (Larson et al., 2004). "The reason for this is likely based on the replication in built forms of many key microsite features that make up the habitat template of natural rock-based ecosystems. Why? Likely because the first buildings were simply extensions of rock walls around the mouths of caves in rocky areas. It would have been easy for species originally restricted to rocky environments to opportunistically exploit the expanding rock-wall habitats created by growing human populations that built more of their own optimal habitats (rock shelters) as they moved out of the caves" (Larson et al., 2004).

The habitat templates represented by rocky areas differ greatly from those of surrounding ecosystems (Larson, Matthes & Kelly, 2000). Areas with an abundance of natural hard surfaces have more extreme hydrological conditions than areas with deeper soil. On natural limestone pavements, for example, where poor drainage causes flooding in the spring and fall, drought can be a severe stressor in the summer due to shallow soils (Stephenson & Herendeen, 1986). Plants in these areas are forced to deal with the combined stresses of flooding and drought within the same growing season. The analogy with urban areas is striking: Urbanization creates similar hydrological challenges due to the increase in hard surfaces from less than 5% prior to urbanization to over 40% in some urbanized regions (Jennings & Jarnagin, 2002). Decreased infiltration in urban areas causes greater amplitudes of flow rates and soil-moisture availability over time—flooding occurs during and immediately after storms, but shallow substrates and water loss due to overland transport result in drier conditions between storms. Green roofs have the capacity to mitigate these effects by replacing hard surfaces with vegetated surfaces, thereby decreasing runoff (Köhler et al., 2002; vanWoert et al., 2005).

Habitat Templates and Green Building Surfaces

It is clear that hard surfaces are responsible for several key environmental impacts of cities, and that these anthropogenic surfaces have analogs in the natural world. Why then should we not look to the vegetation of natural hard-surfaced areas for guidelines in mitigating the impacts of urban areas? (See Table 1 for references to studies describing the natural vegetation of many of the world's shallow-substrate environments). The ability of green roofs to reduce stormwater runoff and insulate buildings depends in part on the depth of the substrate and corresponding vegetation biomass. But there is a trade-off between the maximization of environmental benefits and the minimization of costs: Increasing substrate depth adds to the cost of implementation, especially if reinforcement is required, and so roofers attempt to minimize load on the roof surface. The need to select plants that can survive in shallow substrates forces us to target specific habitat templates. Many green roof species are already drawn from European limestone pavements and dry meadows because they can tolerate harsh rooftop conditions (Dunnett & Kingsbury, 2004). Plants in the genus *Sedum*, long the favorites of green roofers, are frequent components of the vegetation of vertical cliffs in Europe and North America (Bunce, 1968; Holmen, 1965; Hotchkiss, Woodward, Muller & Medley, 1986).

Some natural rock outcrops are largely devoid of vegetation; however, they may still support plant life where cracks, ledges, and other microtopographic features permit the accumulation of organic matter. Other types of natural rock outcrops can have almost full cover of vegetation in shallow soils over bedrock (Catling & Brownell, 1995). The adoption of rock outcrop plants on green roofs would thus mimic a particular kind of outcrop—one where vegetation cover is maximized but total biomass production is limited by shallow substrate. An additional constraint is that while some rock outcrop habitats undergo succession and gradually change into other habitats, such as forest (Burbanck & Phillips, 1983), green roofs are kept permanently at an early stage of succession, either by the extreme stress of shallow substrates or, in deeper media, by the selective removal of woody vegetation. A typical shallow-substrate extensive green roof thus is a manifestation of a very particular habitat template (Figures 2a–2c). Other aspects of the habitat template of natural rock outcrop ecosystems have also been incorporated into green roof designs. Spatial heterogeneity in substrate characteristics is a hallmark of natural rock outcrops (Larson et al., 1989, 2000; Catling & Brownell, 1995; Lundholm & Larson, 2003). While most green roofs feature a uniform substrate, recent initiatives have incorporated spatial heterogeneity in the form of varied soil depths in order to increase species diversity in the vegetation and provide a greater range of habitats for invertebrates (Brenneisen, 2004).

Green facades can also be examined through the habitat-template lens. The vegetation that spontaneously colonizes stone walls can be drawn from a variety of habitats but is dominated by cliff and rock outcrop species (Rishbeth, 1948; Woodell, 1979). The design of walls and other vertical surfaces determines the degree to which plants can grow on them: Building material, degree of shading, aspect, and the presence of microtopography determine the available niche space, much as they do on natural cliffs (Rishbeth, 1948; Larson et al., 2000). The development of green walls or facades is thus a deliberate manipulation of the habitat template to maximize vegetation cover for the purpose of visual relief, building energy savings, or other benefits (von Stülpnagel, Horbert & Sukopp, 1990).

Current attempts to find effective green roof plants revolve around testing species for their tolerance of drought and their ability to survive and spread on green roof substrates (Monterusso, Rowe & Rugh, 2005). Examination of the original habitats of these species shows that they share their living space with a variety of other organisms that together constitute the "vegetation": bryophytes, lichens, and algae. Of particular interest to the green roof industry may be the cryptogamic crusts that form in a variety of horizontal and vertical barrens (Catling & Brownell, 1995; Quarterman, 1950; Schaefer & Larson, 1997). These tend to be dominated by cyanobacteria, which form mats when water is plentiful. Some of the species that occur in these systems have the ability to fix nitrogen and may also play a role in soil stability (West, 1990; Belnap & Gillette, 1998). In shallow-substrate green roof systems, it is possible that these cryptogamic mats can contribute directly to the desired functions of green roofs by cooling the roof surface and retaining water.

The key driving force in plant selection for extensive green roofs has been to find plants that can survive and proliferate in very shallow soil environments. While current plantings often feature polycultures of individually selected species, there has been no work on the role of plant species diversity per se on the functioning of green roofs. Research in other plant communities has identified the potential for larger amounts of species diversity to positively affect ecosystem functions such as biomass production, stability, and nutrient retention or absorption (Tilman et al., 1997, 2001). In general, a community with more species might more completely utilize existing resources due to niche complementarity, which allows the coexistence of species that can use different forms of resources or exhibit resource consumption at different times of the year. In a green roof context, the consumption of water by plants is likely not to be fast enough to make a difference during heavy storms, but for lighter rain events, greater plant uptake of water might decrease runoff. On the other hand, there may be a danger of drought if water consumption occurs more rapidly in more diverse communities. The only study to test this in a simulated green roof environment found no relationship between species diversity and water uptake (Dunnett, Nagase, Booth & Grime, 2005), so it remains to be demonstrated that green roofs with more species function differently than species-poor roofs.

The emerging green roof industry relies on a set of tried-and-true plants that can tolerate the harsh conditions of rooftops. These tend to be succulents from the Crassulaceae, or stonecrop family. A current international trend in green roof horticulture is to begin incorporating regionally appropriate native plants on green roofs (e.g., Monterusso et al., 2005). Certain green roof functions, such as wildlife habitat provision, might also be enhanced by the use of native species. Native insects may be more attracted to native green roof vegetation due to the provision of appropriate food sources or pollen resources. The use of native species that can tolerate harsh conditions is welcome in any urban greening project, providing aesthetically pleasing and educationally valuable biodiversity in hard-surfaced environments that are typically low in biodiversity (McKinney, 2002).

The design of vegetated surfaces on buildings has largely proceeded from engineering considerations, with a more recent focus on the horticultural requirements of desired species. The growing interest in—and potential environmental and economic benefits of—using entire communities of plants on green buildings necessitates a more nuanced understanding of the habitat templates we design and the relationships between community structure, environmental conditions, and ecosystem functions. These concerns must move research on building-surface vegetation into the forefront of current progress in fundamental ecological research.

Acknowledgments

I thank Doug Larson for comments on the manuscript and discussion of these ideas. I also thank Erica Oberndorfer, Jeff Licht, Karen Liu, the members of the Green Roofs for Healthy Cities research committee, and two anonymous reviewers for critical discussion and support.

Literature Cited

Adam, P., Stricker, P., Wiecek, B.M. & Anderson, D.J. (1990). The vegetation of sea cliffs and headlands in New South Wales, Australia. *Australian Journal of Ecology, 15*, 515–547.

Aey, W. (1990). Historical approaches to urban ecology. In H. Sukopp, S. Hejny, and I. Kowarik (Eds.), *Urban ecology* (pp. 113–129). The Hague: SPB Academic Publishing.

Akhani, H. & Ziegler, H. (2002). Photosynthetic pathways and habitats of grasses in Golestan National Park (NE Iran), with an emphasis on the C_4-grass-dominated rock communities. *Phytocoenologia, 32*, 455–501.

Alberti, M., Marzluff, J.M., Shulenberger, E., Bradley, G., Ryan, C. & Zumbrunnen, C. (2003). Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. *BioScience, 53*, 1169–1179.

Alves, R.J.V. & Kolbek, J. (1993). Penumbral rock communities in campo-rupestre sites in Brazil. *Journal of Vegetation Science, 4*, 357–66.

Arbeláez, M.V. & Duivenvoorden, J.F. (2004). Patterns of plant species composition on Amazonian sandstone outcrops in Colombia. *Journal of Vegetation Science, 15*, 181–188.

Ashton, D.H. & Webb, R.N. (1977). The ecology of granite outcrops at Wilson's Promontory, Victoria. *Australian Journal of Ecology, 2*, 269–96.

Bartlett, R.M. & Larson, D.W. (1990). Organization of the Niagara Escarpment cliff community. II. Characterization of the physical environment. *Canadian Journal of Botany, 68*, 1931–41.

Baskin, J.M., Webb, D.H. & Baskin, C.C. (1995). A floristic plant ecology study of the limestone glades of northern Alabama. *Bulletin of the Torrey Botanical Club, 122*, 226–242.

Belnap, J. & Gillette, D.A. (1997). Disturbance of biological soil crusts: impacts on potential wind erodibility of sandy desert soils in SE Utah, USA. *Land Degradation and Development, 8*, 355–362.

Brenneisen, S. (2004). From biodiversity strategies to agricultural productivity. In *Proceedings of the Second North American Green Roof Conference: Greening Rooftops for Sustainable Communities*, Portland, OR, 2–4 June, 2004 (pp. 475–566). Toronto: The Cardinal Group.

Bunce, R.G.H. (1968). An ecological study of Ysgolion Duon, a mountain cliff in Snowdonia. *Journal of Ecology, 56*, 59–75.

Burbanck, M.P. & Phillips, D.L. (1983). Evidence of plant succession on granite outcrops of the Georgia Piedmont. *The American Midland Naturalist, 45*, 292–306.

Burbanck, M.P. & Platt, R.B. (1964). Granite outcrop communities of the Piedmont plateau in Georgia. *Ecology, 45*, 292–306.

Camp, R.J. & Knight, R.L. (1997). Cliff bird and plant communities in Joshua Tree National Park, California, USA. *Natural Areas Journal, 17*, 110–17.

Catling, P.M. & Brownell, V.R. (1995). A review of the alvars of the Great Lakes region: distribution, floristic composition, biogeography and protection. *The Canadian Field-Naturalist, 109*, 143–171.

Chin, S.C. (1977). The limestone hill flora of Malaya I. *Garden's Bulletin, Singapore, 30*, 165–219.

Collins, J.P., Kinzig, A., Grimm, N.B., Fagan, W.F., Hope D., Wu J. & Borer, E.T. (2000). A new urban ecology. *American Scientist, 88*, 416–425.

Collins, S.L., Mitchell, G.S. & Klahr, S.C. (1989). Vegetation-environment relationships in a rock outcrop community in southern Oklahoma. *American Midland Naturalist, 122*, 339–348.

Cox, J.E. & Larson, D.W. (1993). Spatial heterogeneity of vegetation and environmental factors on talus slopes of the Niagara Escarpment. *Canadian Journal of Botany, 71*, 323–32.

Davis, P.H. (1951). Cliff vegetation in the eastern Mediterranean. *Journal of Ecology, 39*, 63–93.

Dunnett, N. & Kingsbury, N. (2004). *Planting green roofs and living walls.* Portland, Oregon: Timber Press.

Dunnett, N., Nagase, A., Booth, R. & Grime, P. (2005). Vegetation and structure and composition significantly influence green roof performance. In *Proceedings of the Third North American Green Roof Conference: Greening Rooftops for Sustainable Communities*, Washington, DC, 4–6 May, 2005. Toronto: The Cardinal Group.

Escudero, A. (1996). Community patterns on exposed cliffs in a Mediterranean calcareous mountain. *Vegetatio, 125*, 99–110.

Fisher, F.J.F. (1952). Observations on the vegetation of screes in Canterbury, New Zealand. *New Zealand Journal of Ecology, 40*, 156–67.

Fuls, E.R., Bredenkamp, G.J. & van Rooyen, N. (1992). Plant communities of the rocky outcrops of the northern Orange Free State, South Africa. *Vegetatio, 103*, 79–92.

Gauld, J.H. & Robertson, J.S. (1985). Soils and their related plant communities on the Dalradian limestone of some sites in central Perthshire, Scotland. *Journal of Ecology, 73*, 91–112.

Gimingham, C.H. & Walton, K. (1954). Environment and the structure of scrub communities on the limestone plateaux of northern Cyrenaica. *Journal of Ecology, 42*, 505–520.

Grubb P.J. (1976). A theoretical background to the conservation of ecologically distinct groups of annuals and biennials in the chalk grassland ecosystem. *Biological Conservation, 10*, 53–76.

Hambler, D.J. (1964). The vegetation of granitic outcrops in western Nigeria. *Journal of Ecology, 52*, 573–94.

Hill, M.O. (2002). Hemeroby, urbanity, and ruderality: bioindicators of disturbance and human impact. *Journal of Applied Ecology, 39*, 708–720.

Holmen, H. (1965). Subalpine tall herb vegetation, site and standing crop. *Acta Phytogeographica Suecica, 50*, 240–248.

Hopper, S.D., Brown, A.P. & Marchant, N.G. (1997). Plants of Western Australian granite outcrops. *Journal of the Royal Society of Western Australia. 80*, 141–158.

Hotchkiss, A.T., Woodward, H.H., Muller, L.F. & Medley, M.E. (1986). Thuja occidentalis L. in Kentucky. *Transactions of the Kentucky Academy of Science, 47*, 99–100.

Ivimey-Cook, R.B. (1965). The vegetation of solution cups in the limestone of the Burren, Co. Clare. *Journal of Ecology, 53*, 437–445.

Ivimey-Cook, R.B. & Proctor, M.C.F. (1966). Plant communities of the Burren, Co. Clare. *Proceedings of the Royal Irish Academy, 64B*, 201–311.

Jackson, G. & Sheldon, J. (1949). The vegetation of magnesian limestone cliffs at Markland Grips near Sheffield. *Journal of Ecology, 37*, 38–50.

Jennings, D.B. & Jarnagin, S.T. (2002). Changes in anthropogenic impervious surfaces, precipitation, and daily streamflow discharge: a historical perspective in a mid-Atlantic subwatershed. *Landscape Ecology 17*, 471–489.

Kassas, M. & Girgis, W.A. (1964). Habitat and plant communities in the Egyptian desert, V: the limestone plateau. *Journal of Ecology, 52*, 107–119.

Köhler, M., Schmidt, M., Grimme, F.W., Laar, M., Paiva, V.L. & Tavares, S. (2002). Green roofs in temperate climates and in the hot-humid tropics—far beyond the aesthetics. *Environmental Management and Health, 3*, 382–391.

Kowarik, I. (1990). Some responses of flora and vegetation to urbanization in central Europe. In H. Sukopp, S. Hejny, and I. Kowarik (Eds.), *Urban ecology* (pp. 45–74). The Hague: SPB Academic Publishing.

Krahulec, F.R.E. & van der Maarel, E. (1986). Preliminary classification and ecology of dry grassland communities on Ölands Stora Alvar (Sweden). *Nordic Journal of Botany, 6*, 797–808.

Kunick, W. (1982). Comparison of the flora of some cities of the central European lowlands. In R. Bornkamm, J.A. Lee, and M.R.D. Seaward (Eds.), *Urban ecology* (pp. 13–22). Oxford, UK: Blackwell Scientific Publications.

Larson, D.W., Matthes, U. & Kelly, P.E. (2000). *Cliff ecology: patterns and process in cliff ecosystems*. Cambridge: Cambridge University Press.

Larson, D. W., Matthes, U., Kelly, P.E., Lundholm, J.T. & Gerrath, J.A. (2004). *The urban cliff revolution.* Toronto: Fitzhenry & Whiteside.

Larson, D.W., Spring, S.H., Matthes-Sears, U. & Bartlett, R.M. (1989). Organization of the Niagara Escarpment cliff community. *Canadian Journal of Botany, 67*, 241–63.

Lundholm, J.T. & Larson, D.W. (2003). Relationships between spatial environmental heterogeneity and plant species diversity on a limestone pavement. *Ecography, 26*, 715–722.

Lundholm, J.T. & Marlin, A. (2006). Habitat origins and microhabitat preferences of urban plant species. *Urban Ecosystems, 9*, 139–159.

Lundqvist, J. (1968). Plant cover and environment of steep hillsides in Pite Lappmark. *Acta Phytogeographica Suecica, 53*, 1–153.

Makirinta, U. (1985). Vegetation types and exposure on acid rocks in south Häme, south Finland. *Colloques Phytosociologiques, Végétation et Géomorphologie, 13*, 469–84.

Malloch, A.J.C., Bamidele, J.F., & Scott, A.M. (1985). The phytosociology of British sea-cliff vegetation, with special reference to the ecophysiology of some maritime cliff plants. *Vegetatio, 62*, 309–18.

McDonnell, M.J., Pickett, S.T.A., Groffman, P., Bohlen, P., Pouyat, R.V., Zipperer, W.C., Parmelee, R.W., Carreiro, M.M. & Medley, K. (1997) Ecosystem processes along an urban-to-rural gradient. *Urban Ecosystems, 1*, 21–36.

McKinney, M.L. (2002). Urbanization, biodiversity, and conservation. *Bioscience, 52*, 883–890.

Michalik, S. (1991). Distribution of plant communities as a function of the relative insolation of the Czyzówki rocky ridge in the Ojców National Park. *Acta Societatis Botanicorum Poloniae, 60*, 327–338.

Monterusso, M.A., Rowe, D.B. & Rugh, C.L. (2005). Establishment and persistence of *Sedum* spp. and native taxa for green roof applications. *HortScience, 40*, 391–396.

Nuzzo, V. (1996). Structure of cliff vegetation on exposed cliffs and the effect of rock climbing. *Canadian Journal of Botany, 74*, 607–617.

Oosting, H.J. & Anderson, L.E. (1937). The vegetation of a barefaced cliff in western North Carolina. *Ecology 18*, 280–292.

Oosting, H.J. & Anderson, L.E. (1939). Plant succession on granite rock in eastern North Carolina. *Botanical Gazette, 100*, 750–768.

Orians, G. (1986). An ecological and evolutionary approach to landscape aesthetics. In E.C. Penning-Rowsell and D. Lowenthal (Eds.), *Landscape meanings and values* (pp. 3–25). London: Allen and Unwin.

Orians, G. & Heerwagen, J.H. (1992). Evolved responses to landscape. In J.H. Barkow, L. Cosmides, and J. Tooby (Eds.), *The adapted mind* (pp. 555–579). Oxford: Oxford University Press.

Pärtel, M., Kalamees, R., Zobel, M., & Rosen E. (1999). Alvar grasslands in Estonia: variation in species composition and community structure. *Journal of Vegetation Science, 10*, 561–568.

Porembski, S., Barthlott, W., Dörrstock, S. & Biedinger, N. (1994). Vegetation of rock outcrops in Guinea: granite inselbergs, sandstone table mountains, and ferricretes—remarks on species numbers and endemism. *Flora, 189*, 315–26.

Quarterman, E. (1950). Major plant communites of Tennessee cedar glades. *Ecology, 31*, 234–254.

Rishbeth, J. (1948). The flora of Cambridge walls. *Journal of Ecology, 36*, 136–148.

Rodwell, J.S. (2000). *British plant communities volume 5: maritime communities and vegetation of open habitats.* Cambridge: Cambridge University Press.

Rodwell, J.S. (1992). *British plant communities volume 2: grasslands and montane* *communities.* Cambridge: Cambridge University Press.

Rutherford, M.C. (1972). Notes on the flora and vegetation of the Omuverume Plateau-mountain, Waterberg, South West Africa. *Dinteria, 8*, 3–55.

Schaefer, C.A. & Larson, D.W. (1997). Vegetation, environmental characteristics, and ideas on the maintenance of alvars on the Bruce Peninsula, Canada. *Journal of Vegetation Science, 8*, 797–810.

Southwood, T.R.E. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology, 46*, 337–365.

Spirn, S.A. (1984). *The granite garden: urban nature and human design.* New York: Basic Books.

Stephenson, S.N. & Herendeen, P.S. (1986). Short-term drought effects on the alvar communities of Drummond Island, Michigan. *The Michigan Botanist, 25*, 16–27.

Stülpnagel, A. von, Horbert, M. & Sukopp, H. (1990). The importance of vegetation for the urban climate. In H. Sukopp, S. Hejny & I. Kowarik (Eds.), *Urban ecology* (pp. 175–193). The Hague: SPB Academic Publishing.

Suren, A.M. & Ormerod, S.J. (1998). Aquatic bryophytes in Himalayan streams: testing a distribution model in a highly heterogeneous environment. *Freshwater Biology, 40*, 697–716.

Tilman D., Knops J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science, 277*, 1300–1302.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science, 294*, 843–845.

VanWoert, N.D, Rowe, D.B., Andresen, J.A., Rugh, C.L., Fernandez, R.T. & Xiao, L. (2005). Green roof stormwater retention: effects of roof surface, slope, and media depth. *Journal of Environmental Quality, 34*, 1036–1044.

West, N.E. (1990). Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. *Advances in Ecological Research, 20*, 179–223.

Wiser, S.K. (1994). High-elevation cliffs and outcrops of the Southern Appalachians: vascular plants and biogeography. *Castanea, 59*, 85–116.

Wittig, R. (2004). The origin and development of the urban flora of central Europe. *Urban Ecosystems, 7*, 323–339.

Woodell, S. (1979). The flora of walls and pavings. In I.C. Laurie (Ed.), *Nature in cities* (pp. 135–156). New York: John Wiley & Sons.

Glossary

Anthropogenic: Caused by humans.

Cryptogamic crust: Mat formed by plants that reproduce by gametes or spores rather than seeds (e.g., algae).

Negative phototropism: Growth away from the direction of a light stimulus.

Riparian: Pertaining to the banks of a stream or river.

Figure 1: A typical suburban front yard. The "suburban savanna" hypothesis ignores the built structure and other hard surfaces as ecological elements in this landscape (photo by J. Lundholm).

Figure 2a–2c: Natural (a), spontaneous urban (b), and designed (c) rock pavement habitats. The natural pavement is a limestone barren on the Bruce Peninsula, in southern Ontario. The designed site is a green roof in Portland, Oregon. (Photos by J. Lundholm)

Table 1. Descriptions of natural vegetation in shallow-substrate environments.

East & Central US	Cedar glades (limestone barrens)	Quarterman 1950, Baskin et al. 1995
Great Lakes	Alvars (limestone barrens)	Catling & Brownell 1995, Schaefer & Larson 1997
South +E US	Granite barrens + cliffs	Oosting & Anderson 1937, 1939, Burbanck & Platt 1964, Collins et al. 1989, Wiser 1994
Southern Ontario, Canada	Limestone cliffs, talus slopes	Larson et al. 1989, Bartlett et al. 1990, Cox & Larson 1993
Illinois US	Limestone cliffs	Nuzzo 1996
SW US	Desert cliffs	Camp & Knight 1997
Ireland	Burren, limestone barrens	Ivimey-Cook 1965, Ivimey-Cook & Proctor 1966
UK	Limestone pavement	Gauld & Robertson 1985
UK	Sea cliffs	Rodwell 2000, Malloch et al. 1985
UK	Inland cliffs	Bunce 1968, Jackson & Sheldon 1949
Sweden, Estonia	Alvars (Limestone grassland, barrens)	Krahulec & van der Maarel 1986
N Sweden	Steep slopes	Lundqvist 1968
S Finland	Acid silicate rocks	Makirinta 1985
Estonia	Alvars (Limestone grassland)	Pärtel et al. 1999
Poland	Rocky ridge	Michalik 1991
E Mediterranean	Cliffs	Davis 1951
W Mediterranean	Calcareous cliffs	Escudero 1996
Colombia	Sandstone outcrops	Arbeláez & Duivenvoorden 2004
Brazil	Shaded cliffs	Alves & Kolbek 1993
Iran	Cliffs, steep slopes, outcrops	Akhani & Ziegler 2002
Egypt, Libya	Limestone plateau	Gimingham & Walton 1954; Kassas & Girgis 1964
Guinea	Rock outcrops, Inselbergs	Porembski et al. 1994
Nigeria	Granitic outcrops	Hambler 1964
S Africa	Rock outcrops	Rutherford 1972, Fuls et al. 1992
Malay Peninsula	Limestone outcrops	Chin 1977
New South Wales, Australia	Sea cliffs	Adam et al. 1990
Western Australia	granite outcrops	Hopper et al. 1997
Victoria, Australia	Granite outcrops	Ashton & Webb 1977
New Zealand	Scree slopes	Fisher 1952